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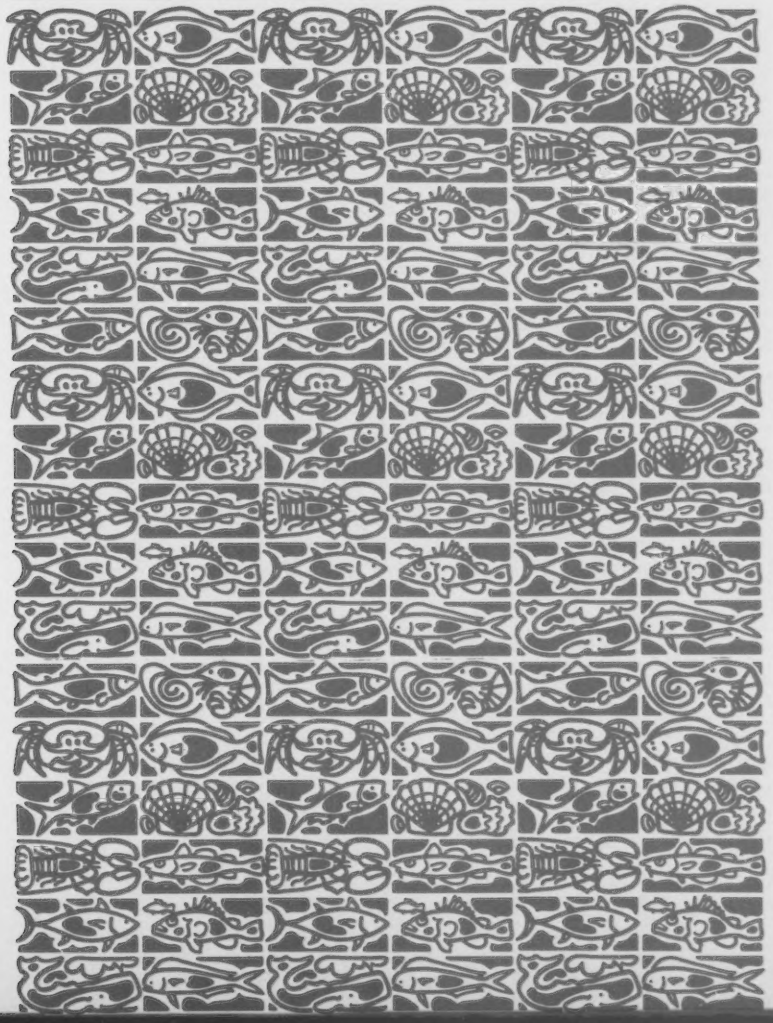

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Publications Awards 1988-89

National Marine Fisheries Service, NOAA

The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the *Fishery Bulletin* volume 87 and *Marine Fisheries Review* volume 50. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles which significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. The following were deemed the best.

Fishery Bulletin 1989

Wallace W. Morse

Catchability, growth, and mortality of larval fishes. *Fishery Bulletin* 87: 417-446. Dr. Morse is with the Sandy Hook Laboratory, Northeast Fisheries Science Center, Highlands, New Jersey.

Marine Fisheries Review 1988

Kenneth N. Baxter, Carlton H. Furr Jr., and Elizabeth Scott

The commercial bait shrimp fishery in Galveston Bay, Texas, 1959-87. *Marine Fisheries Review* 50(2):20-28. Dr. Baxter, Dr. Furr, and Ms. Scott are with the Galveston Laboratory, Southeast Fisheries Science Center, Galveston, Texas. Dr. Furr has since retired from his position with the National Marine Fisheries Service.

Abstract.–Northern shrimp *Pandalus borealis* carapace length-frequency data collected from shrimp surveys and commercial catches between 1972 and 1986 were studied to estimate age, growth, and mortality in Pavlof Bay, Alaska. Dominant size modes representing 1971 and 1975 year-classes were separated from carapace length-frequency distributions by the use of a maximum-likelihood separation technique. The growth rate for the 1975 year-class was significantly greater than that of the 1971 year-class. Because the abundance of the 1975 year-class was lower than that of the 1971 year-class, an inverse relationship of growth to year-class strength was suggested. Age-at-sex transition appears to be related to year-class abundance or overall density as 1975 year-class shrimp completed transition at a younger age than that of 1971. Increases in natural mortality occurred after the 1971 year-class completed transformation to the female sex at age 6.4, and may indicate a combination of spawning stress and senescence or increasing abundance of the predator, Pacific cod *Gadus macrocephalus*. Dynamic pool yield-per-recruit analysis indicated maximum biomass of year-classes was achieved at or prior to full recruitment to the survey and commercial fishing gear. Because mortality rates are high, yield-per-recruit is optimized by harvesting more of the smaller male shrimp.

Manuscript accepted 5 July 1991.
Fishery Bulletin, U.S. 89:541–553 (1991).

Age, Growth, and Mortality of the Northern Shrimp *Pandalus borealis* Kröyer in Pavlof Bay, Alaska

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The Alaska Peninsula region of the western Gulf of Alaska was the site of one of the world's major shrimp fisheries in the 1970s (Anderson and Gaffney 1977). A significant decline in shrimp abundance starting in 1978 lead to the closure of most areas to fishing in 1979, and to date the fishery has yet to reopen. The cause of this decline and the failure of stocks to recover to fishable levels are obscured by a lack of information on the population dynamics of pandalid shrimps in the western Gulf of Alaska. In an effort to fill this information gap, I have estimated the age, growth, and mortality of two year-classes from a stock of northern shrimp *Pandalus borealis* Kröyer, the major commercial species in the region.

The Pavlof Bay (Fig. 1) stock of *P. borealis* was chosen for this study because it has supported a major fishery and an extensive database was available. The Bay was a major producer accounting for over 13,000 metric tons (t) of pandalid shrimp landings in 1977 alone. *Pandalus borealis* made up 11–97% of landings, with variable quantities of *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* making up the remainder. Pavlof Bay shrimp have been surveyed annually by the National Marine Fisheries Service (NMFS) since 1972. Data collected from these surveys include weight, number, and carapace length-frequencies by sex for *P. borealis*. The Alaska Department of Fish and Game (ADF&G) has collected species and size-composition data from commercial landings since the beginning of the fishery in 1968.*

Pandalus borealis in Pavlof Bay are managed as a discrete stock by the ADF&G. Analysis of data from commercial catches and shrimp surveys conducted by NMFS and ADF&G suggest that migration between adjacent bays along the Alaska Peninsula is minimal (Jackson et al. 1983). Vertical migrations in concert with ocean currents may act as dispersal mechanisms for pandalids (Barr 1970, Pearcy 1970, Gotshall 1972). In Pavlof Bay, effects of ocean currents probably are minimized by barrier islands and shallow entrances that favor confinement and limit immigration (Fig. 1).

Since there are no known anatomical structures for ageing *P. borealis*, researchers have used length-frequency analysis to estimate age and growth. For example, Rasmussen (1953) used dominant year-class modes to interpret growth and sex transformation of *P. borealis* in Norwegian stocks, and Skúladóttir (1981) used the positive deviations from long-term length-frequency distributions to identify average lengths-at-age for *P. borealis* from Icelandic fjords.

* Commercial landings, species, and size composition data available from Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615.

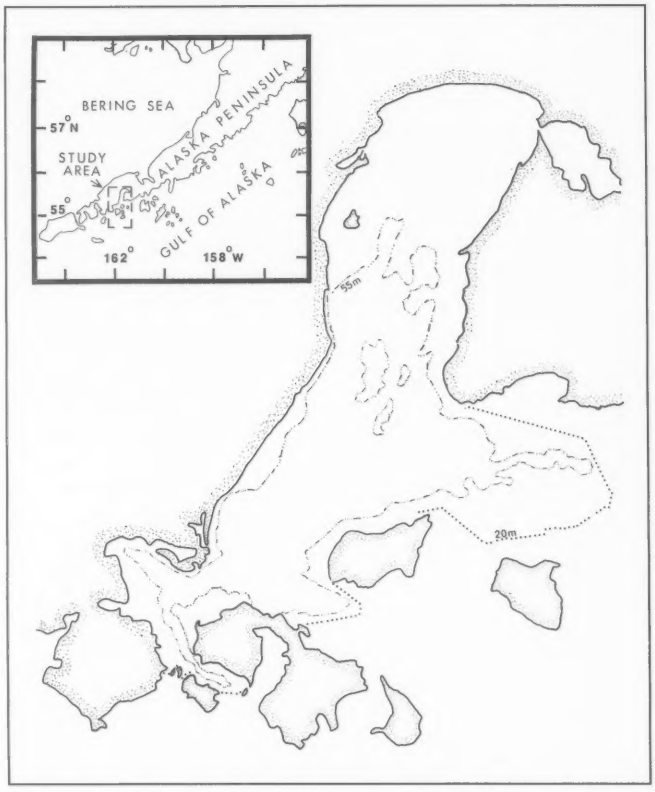

Figure 1
Pavlof Bay, Alaska, sampling area showing 55 m isobath (dotted/dashed line) and approximate location of the 20 m isobath (dotted).

I have separated the dominant size modes representing year-classes from Pavlof Bay length-frequency distributions using the maximum-likelihood technique of Macdonald and Pitcher (1979). Annually, calculated mean lengths and numerical abundance of year-classes were then used to estimate growth and mortality using methods similar to those of Fréchette and LaBonté (1981) and Anderson (1981). The present study expands on previous work by using modal analysis of length-frequencies from commercial catches to estimate fishing and natural mortality rates. Results from these analyses were used to examine the yield-per-recruit function in relation to mortality and growth as well as year-class strength.

Materials and methods

Pavlof Bay was surveyed annually from 1972 to 1986 by trawling at randomly selected stations from August to mid-September (Table 1). During these months dense aggregations of *P. borealis* form in relatively deep water prior to mating and spawning. Earlier surveys had shown that shrimp concentrate in depths greater than 70 m (Ronholt 1963). Consequently, all survey tows were restricted to depths greater than 55 m (Fig. 1). Each year, except 1973, 10 to 13 randomly selected (with replacement) locations were chosen from a grid of the Bay's shrimp habitat divided into 22 stations (~13.7 km^2 each). Sampling was conducted with a 30-minute tow (~1.8 km) during daylight using a 32 mm mesh (32 mm mesh codend liner) high-opening shrimp trawl with an 18.6 m headrope and footrope (Wathne 1977). The mesh size and configuration of this trawl were similar to commercial fishing gear which allowed for direct comparison between survey and commercial data.

Carapace lengths (CL) were measured to the nearest 0.5 mm (eye socket to midposterior carapace edge) for approximately 300 specimens of *P. borealis* selected at random

Table 1
Biomass estimates and commercial landings (catch) of *Pandalus borealis* shrimp in Pavlof Bay, 1972–86 (metric tons with 80% confidence intervals for biomass; catches removed prior to next research survey).

Dates	No. tows	Biomass[1] (mt)	Catch[2] (mt)
7–10 Sep 1972	10	8,310 (6,999–9,616)	177
13 Sep 1973[3]	2	3,084 (3,062–3,107)	1,075
8–10 Sep 1974	13	11,476 (10,406–12,546)	150
19–21 Sep 1975	12	6,886 (5,597–8,174)	1,919
12–14 Sep 1976	12	10,796 (9,086–12,501)	5,670
25–27 Aug 1977	13	12,392 (9,462–15,318)	3,819
29–30 Aug 1978	13	3,602 (2,880–4,323)	826
4–7 Sep 1979	10	599 (367–830)	Closed
24–26 Aug 1980	12	549 (376–721)	Closed
10–11 Sep 1981	12	662 (485–839)	Closed
19–21 Aug 1982	13	749 (485–1,014)	Closed
11–12 Aug 1983	12	2,646 (2,094–3,197)	Closed
29–30 Aug 1984	13	308 (176–463)	Closed
12–15 Aug 1985	12	617 (397–838)	Closed
28 Aug–1 Sep 1986[4]	13	2,315 (1,631–3,020)	Closed

[1] Biomass estimates and confidence intervals were calculated by the "area swept" technique of Alverson and Pereyra (1969), using the equations developed by Smith and Bakkala (1982).
[2] Catches calculated from commercial samples and total pandalid catch (Albers and Anderson 1985).
[3] Survey curtailed due to severe weather.
[4] A 3.2 mm mesh liner was used during this survey.

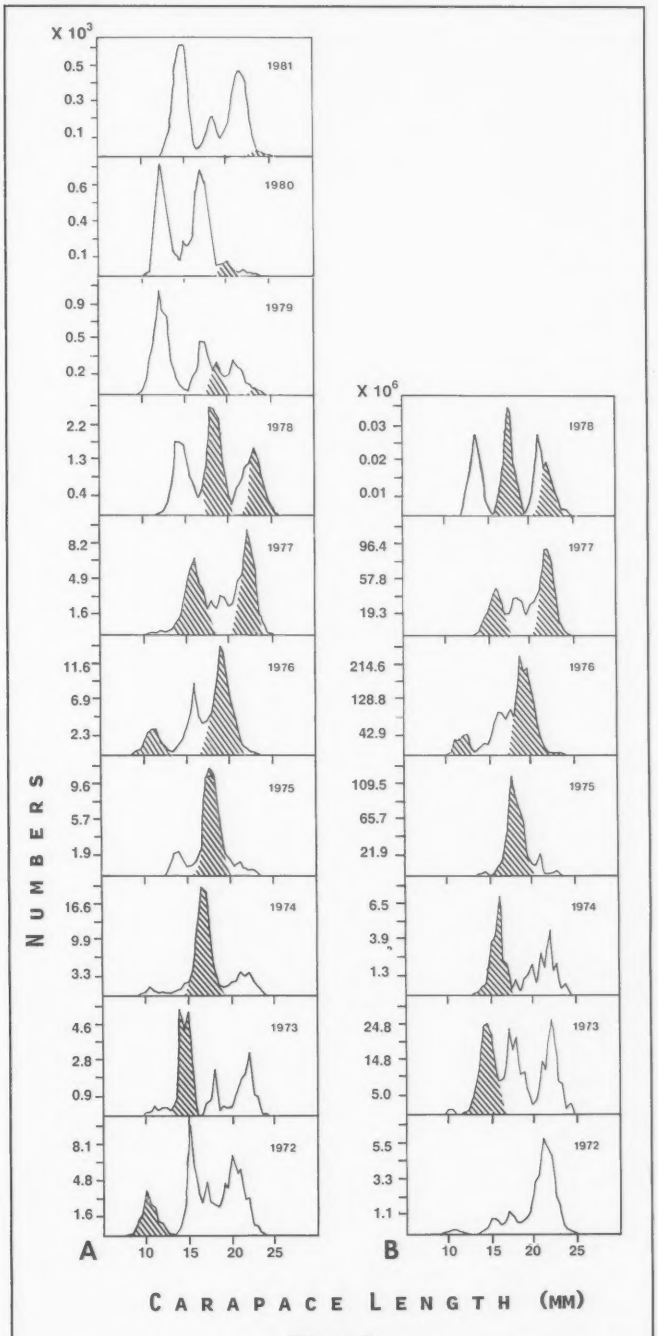

Figure 2
Size-frequency distributions of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from (A) annual research surveys, 1972–81, and (B) total numbers in the commercial catch, 1972–78. Dominant 1971 and 1975 size modes are shaded.

from each survey tow. Endopodite structure of the first two pleopods (Allen 1959) was used to separate the sexes. Length-frequency data by sex from commercial catch samples were provided courtesy of the ADF&G (211 Mission Rd., Kodiak, AK 99615).

Estimating mean size and abundance of year-classes

The total number of *P. borealis* in a survey or commercial catch was estimated for each 0.5 mm CL group as

$$\hat{N}_{ij} = n_{ij} \frac{C_j}{w_j} \qquad (1)$$

where

$\hat{N}_{ij}$ = number of *P. borealis* in the ith size interval taken in the jth haul (i = 1....q; j = 1....r),

n_{ij} = number of *P. borealis* in the ith size interval sampled from the jth haul,

C_j = weight of *P. borealis* in the jth haul, and

w_j = sampled weight in the jth haul.

Estimates of abundance for each size group were summed for all tows annually to form length-frequency distributions (Fig. 2). The technique of Macdonald and Pitcher (1979) was then used to separate and quantify year-class modes. Length was assumed to be normally distributed for a given year-class. The computer algorithm (Macdonald 1980) requires starting values of parameters (mean, standard deviation, proportion) for each component (year-class). Starting values for parameters were visually determined and the program iteratively computed maximum-likelihood parameters.

The estimated number of shrimp of a given year-class ($\hat{N}_k$) was calculated as

$$\hat{N}_k = \hat{P}_k \hat{N}.. \quad \hat{B} / \sum_{j=1}^{r} C_j, \qquad (3)$$

letting

$\hat{P}_k$ = estimated proportion of the kth year-class in the sample population N..,

$\hat{N}..$ = estimated total number of shrimp captured in a survey period, and

$$\hat{B} = \frac{A}{r} \sum_{j=1}^{r} [C_j/a_j]\, q, \quad (3)$$

where $\hat{B}$ = estimated biomass of *P. borealis*,
A = total survey area (Pavlof Bay >55 m; 302 km^2),
a_j = area covered in tow j, and
q = catchability coefficient of the sampling gear.

In the absence of better information, the catchability coefficient (q) in this analysis was set at 1.0. Strictly speaking, this only applies to shrimp sizes that are fully recruited to the sampling area and gear. Equation (3) is modified from Alverson and Pereyra (1969). Biomass estimates are conservative because small (<18 mm CL) shrimp are not fully vulnerable to capture.

Finally, the number of *P. borealis* of a given year class ($\hat{R}_k$) caught by the fishery between research sampling surveys was estimated as

$$\hat{R}_k = \hat{P}_k\, N..\, [L/W], \quad (4)$$

where $\hat{P}_k$ is calculated similarly to survey catches above,
$N..$ = total number of shrimp sampled from the commercial catch in a given year,
L = total landed weight of *P. borealis* between surveys, and
W = total sample weight from which $N..$ was calculated.

Determination of growth and mortality

Growth rates were estimated by following the 1971 and 1975 year-classes through a time series of length-frequency distributions (Fig. 2). The dominance of these year-classes minimizes the effect of overlap with adjacent modes. Nonlinear least-squares regression (Program BCG2, Abramson 1971) was used to fit von Bertalanffy growth curves to average size-at-age data.

Annual instantaneous total mortality rates (Z) for the dominant year-classes were calculated as

$$Z_k = -\ln (N_{k,t+1} / N_{k,t}) \quad (5)$$

where t = one year and $N_{k,t}$ and $N_{k,t+1}$ represent the relative abundance of the kth year-class in two consecutive years.

Estimated fishing (F) mortality was derived from estimated total mortality using Ricker's (1975) formula

$$F_k = \hat{\mu}\, Z_k / (1 - e^{-Z_k}) \quad (6)$$

where $\hat{\mu}$ = annual exploitation, the ratio of estimated catch in numbers (R_k from eq. 4) and estimated abundance (N_k from eq. 2) of the 1971 and 1975 year-classes.

Natural mortality (M) was calculated by subtraction:

$$M_k = Z_k - F_k. \quad (7)$$

Results and discussion

Estimates of age, growth, and mortality rates in this study were made for two dominant year-classes that could be followed through most of their life span. Assumptions underlying the estimates were that size modes represented year-classes, and immigration and emigration of Pavlof Bay shrimp were minimal.

Identification of year-classes

The 1971 and 1975 year-class modes were identified and followed through 1981 in length-frequency plots (Fig. 2, Table 2). The size at which dominant modes are first identified is between 10 and 11 mm CL. *Pandalus borealis* of this size are approximately 1.4 years old if it is assumed that larvae hatch in April, and early growth is similar to that reported by other investigators (Butler 1964, Ivanov 1970, Fox 1972, Skúladóttir 1981). The plots indicate similar patterns between the two year-classes, as well as close agreement in location of dominant modes in both the survey and commercial data (Fig. 2 and Table 2). Close agreement in the modal structure of the two independent data sets supported the assumption that the survey and commercial catch data were drawn from the same population and made estimation of fishing mortality possible. Commercial gear used comparable mesh and had a similar fishing configuration to our survey gear, except for the codend liner. The presence of a codend liner in survey sampling gear may explain the better definition of 1.4 year-old modes in survey samples due to the smaller effective mesh size.

Problems in identifying the age of the smallest modal group have been noted by other researchers (Fréchette and Parsons 1983). Entering year-class modes from survey data were assigned the age of 1.4. A smaller mode (mean of 6.5–7.5 mm CL; numbers not large enough to be depicted in Fig. 2) was designated age 0.4 (~146 days assuming an April hatch). Nunes (1984) reported that laboratory-reared *P. borealis* postlarvae reached 3.6–3.9 mm CL by about 110 days after hatch-

Table 2

Mean carapace length (CL), standard deviation (SD), and estimated number in survey area or estimated number caught in millions (N) of domination year-class components separated by the Macdonald and Pitcher (1979) method from Pavlof Bay, Alaska, trawl survey and commercial catch length-frequency samples.

	1971 year-class						1975 year-class					
	Survey			Commercial catch			Survey			Commercial catch		
	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$
1972	10.06	0.79	388.48	10.24	0.75	0.78						
1973	14.28	0.55	561.33	14.16	0.79	98.30						
1974	16.47	0.73	2337.62	15.54	0.70	21.93						
1975	17.44	0.71	1252.43	17.65	0.72	450.55						
1976	18.96	0.87	1738.33	19.10	0.91	642.08	10.66	0.81	413.90	11.01	0.49	53.33
1977	21.75	0.99	1007.98	21.67	0.85	184.36	15.68	0.93	225.03	14.74	0.68	26.70
1978	22.98	0.84	177.96	22.17	0.48	21.56	18.20	0.90	317.99	17.17	0.56	71.44
1979	23.61	0.67	3.93				19.23	0.79	23.63			
1980							21.45	0.60	9.83			
1981							23.01	1.17	3.48			

ing. Seasonal trawl sampling and larval surveys at Chiniak Bay, Alaska, showed juvenile young-of-the-year reaching an average size of 7 mm CL by September (~153 days after hatching) for three consecutive years (E. Munk, Kodiak Lab., Alaska Fish. Sci. Cent., pers. commun., 10 June 1987). Since no other modes were found between this juvenile group and the larger-age 1.4 mode in survey sampling, it was assumed the age designation of these groups was correct. Skúladóttir (1981) found difficulty in assigning ages to entering size modes (average size 10–12 mm CL), probably because the stretched mesh gradually increased from 32 to 38 mm over five years of sampling (Hallgrímsson and Skúladóttir 1981). Fréchette and LaBonté (1981) also noted a similar problem with a mesh size of 38 mm. The mesh size in this study was 32 mm with a 32 mm codend liner, which may have helped in the retention of young shrimp.

Table 3

Average number of *P. borealis* caught per survey tow 1972–86. Tow length standardized to one nautical mile (1.85 km).

Survey	Number	Survey	Number
1972	160,752	1980	11,521
1973	61,410	1981	10,370
1974	208,356	1982	2,780
1975	126,322	1983	11,679
1976	199,566	1984	1,209
1977	160,074	1985	3,524
1978	49,879	1986	11,488
1979	16,066		

Abundance and variability of year-classes

The estimated biomass of *P. borealis* in Pavlof Bay peaked in 1977 and declined substantially in later years (Table 1). In response to reduced biomass, the fishery was closed by the ADF&G in 1979; the population subsequently stabilized at a lower level after 1978. The decline in abundance of the 1971 year-class (Table 2) reflected that of the total population (Table 1). The average number of *P. borealis* caught per survey tow declined steadily from approximately 199,000 in 1976 to 10,000 in 1981 (Table 3).

Dominant year-classes persisting in the population result from favorable conditions during their embryonic, larval, or juvenile stages. The relationship of shrimp landings to water temperatures prevailing during the spawning period 2 years earlier has been demonstrated in Gulf of Maine stocks (Dow 1966). Eggs incubated at 3 and 6°C resulted in larger newly hatched *P. borealis* larvae (1.41–1.49 mm CL) than those incubated at 9°C (1.09 mm CL) (Nunes 1984). If larger newly hatched larvae have a survival advantage, then colder incubation temperatures (6°C or lower) might enhance year-class strength. Warm temperatures may lead to lower survival of eggs and larvae of *P. borealis* due to increased egg parasitism and reduced food conversion efficiency (Paul and Nunes 1983). Minimum seawater temperatures in the study area normally range from 3 to 6°C (McLain et al 1979). Royer (1989) examined temperatures across the Gulf of Alaska and found very low-frequency fluctuations of ±2.0°C occur in the upper 250 m of the water column north of 55°N in the Gulf of Alaska (including Pavlof Bay). A cold temperature anomaly of more than 1.2°C was reported for the 1971–78 period in this region. These

anomalous low temperatures may have played a part in the formation of the strong 1971 and 1975 year-classes. Conversely, the relatively warm temperatures since 1980, perhaps peaking in 1984 (Royer 1989), may explain the lack of large year-classes in later years (Figs. 2, 3). It is possible that surveys of larval or juvenile abundance and related environmental parameters, mainly temperature, could be used to forecast future abundance trends.

Extreme variability in year-class strength can mean the success or failure of the commercial fishery. The 1971 year-class was dominant in commercial catches in Pavlof Bay during at least five fishing seasons (Fig. 2B). To calculate the contribution of dominant year-classes to the commercial catch, an average total weight, calculated from Pavlof Bay *P. borealis* length-weight data, $W = 0.00104\ CL^{2.70160}$ (Anderson 1981) was multiplied by the estimated number caught in each year-class (Table 2). During the years 1974–78, the 1971 year-class contributed about 70% and the 1975 year-class about 3% of the 12,384 metric tons of *P. borealis* harvested from Pavlof Bay. Although the commercial fishery was closed in Pavlof Bay from 1979 to 1986, little or no improvement in stock condition occurred. In Pavlof Bay, it appears that the *P. borealis* fishery was largely supported by a single year-class.

Estimates of growth

Estimates of growth parameters in this study were generated only from the two dominant year-classes that could be followed through a time series (Fig. 2). Growth estimates depend heavily on the occurrence and definition of modes. *Pandalus borealis* have a synchronous and relatively abbreviated hatching period which gives rise to fairly well-defined size modes shortly after settlement of juveniles (Fréchette and Parsons 1983). Survey sampling was conducted in August–September, toward the end of the period of rapid summer growth. Studies that have continuously sampled throughout the spring and summer show growth slows in late summer, possibly as the result of spawning. Some instar growth is possible, however, even during mating and spawning, for the more frequently molting young males. I interpret the double-spike top of the 1971 year-class depicted in the 1973 survey data (Fig. 2A) as possibly representing year-class instar growth. As the shrimps age and transform to females, molting is reduced to perhaps two times a year, into and out of breeding dress (Allen 1959). Mode definition for year-classes after they become female is therefore not beset with an interpretation problem resulting from instar growth. The additional problem of overlap with adjacent but minor modes, especially with slower-growing females, is not so acute when using only dominant year-classes for growth estimates.

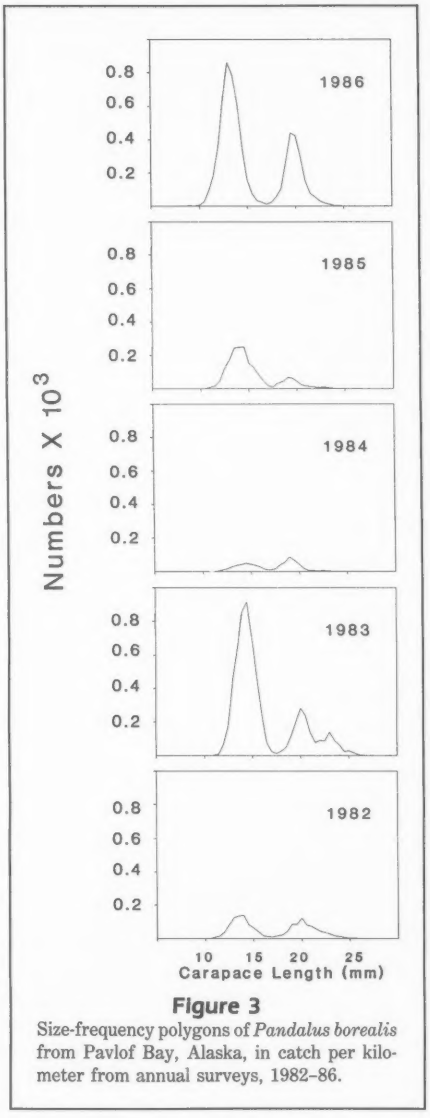

Figure 3
Size-frequency polygons of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from annual surveys, 1982–86.

Separate von Bertalanffy growth curves were fit to average size-at-age data for the two dominant year-classes (Fig. 4). Parameters of the fitted relationship were $L_\infty = 29.64$, $K = 0.16$, and $t_0 = -1.30$ for the 1971 year-class, and $L_\infty = 26.31$, $K = 0.29$, and $t_0 = -0.47$ for the 1975 year-class. A Friedman two-way analysis of variance by ranks (Connover 1971) showed that members of the 1975 year-class were significantly ($P<0.001$) larger for a given age, indi-

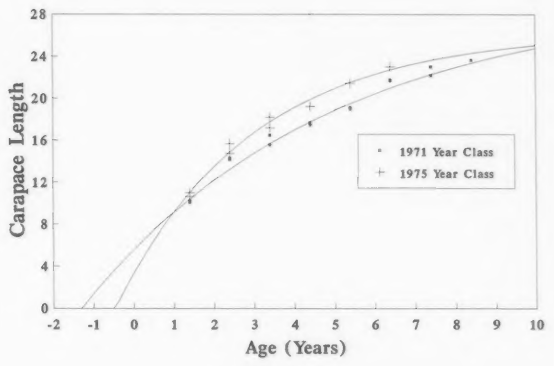

Figure 4

Von Bertalanffy growth curves generated from 1971 and 1975 year-class *Pandalus borealis* mean size-at-age data from both survey and commercial catch data.

Table 4

Mean size (CL) and standard deviation (SD) of 1.4 year-old *P. borealis* from 1972–86 survey samples in Pavlof Bay, Alaska.

Survey year	CL	SD
1972	10.06	0.79
1973	11.39	0.92
1974	10.62	0.92
1975	10.99	0.67
1976	11.84	1.98
1977	11.52	0.94
1978	11.72	0.70
1979	11.75	0.70
1980	13.21	0.83
1981	14.41	0.74
1982	13.70	1.12
1983	14.31	0.99
1984	13.97	1.24
1985	13.45	1.09
1986	13.24	1.04

cating a higher growth rate for this year-class. For example, the 1971 year-class attained average sizes of 16.47 and 21.75 mm CL at ages 3.4 and 6.4, respectively, whereas the 1975 year-class averaged 18.20 and 23.01 mm CL at these ages. Skúladóttir (1981) also detected large differences in growth rates between year-classes. In her study, one slow-growing year-class had a $K = 0.15$ and $L_\infty = 28$ which is similar to the parameters calculated for the 1971 year-class in this study. On the other hand, parameters calculated for the average of five fast-growing year-classes in her study indicated a $K = 0.23$ which is lower than the K (0.29) calculated for the 1975 year-class in the present study.

While growth of *P. borealis* is probably not related to overall population density, there is evidence of an inverse relationship relative to within year-class strength. Both the 1971 and 1975 year-classes hatched during periods of high overall population levels (Table 1), but the faster early growth of the 1975 year-class may be explained by its relatively lower abundance (Table 2) and, presumably, reduced competition for food during the juvenile phase. *Pandalus borealis* is an aggregating species exhibiting differential distribution by size, sex, age, and season (Shumway et al. 1985). Although most larvae are captured between 20 and 30 m in the water column (Haynes 1983), Wolotira et al. (1984) report a downward shift in vertical distribution with progressive stages of larval development. They theorized distribution differences reflect either a change in diet or distribution of food items. Berkeley (1930) also describes the apparent segregation of juveniles from the adult population. The effect of ecological separation of life-history stages could, therefore, explain differing growth rates among year-classes even though overall population density was high.

Since 1979, the occurrence of small shrimp (<12 mm CL) in survey samples has been much less than in previous years (Figs. 2A, 3). Three possible explanations for the virtual disappearance of this size-class are (1) small shrimp may only be retained when overall catch rates are as high as they were in 1972–77, (2) juvenile shrimp may not normally be found within the same area as larger adult shrimp except when high population levels force them into the less-preferred adult habitat, and (3) faster growth of juvenile shrimp may have led to entering year-classes growing beyond 10 mm CL to 13–15 mm CL since 1979. I believe the most plausible explanation for the disappearance of small shrimp from survey samples is faster growth of juveniles. Results of this study suggest growth is inversely related to year-class strength. The overall population decline of *P. borealis* in Pavlof Bay (Table 1) is attributed to the dying out of the relatively strong 1971 and 1975 year-classes and a series of relatively weak entering year-classes since 1979 (Figs. 2, 3). The 1.4 year-old group is now between 13.2 and 14.4 mm CL rather than the 10–11.8 mm CL that was observed for 1972–79 survey samples (Table 4). The possibility of missing size modes in this recent data series is low because sample sizes remained large (about 5000 shrimp per survey). Independent sampling of shrimp length frequency from cod stomachs captured in 1980 and 1981 trawl surveys showed cod consume smaller shrimp, probably the 0.4 year-olds (6.5 mm CL), than were found in trawl samples (Albers and Anderson 1985). Beyond 10 mm

CL, length frequencies were similar for both cod and trawl data, suggesting that the age designation of this larger 1.4 mode is correct.

Variability in growth rates of year-classes also causes variability in the age of full recruitment in survey sampling, owing to the size selectivity of our 32 mm mesh trawl. Recruitment was complete at ages 5.4 and 3.4 (18.96 and 18.20 mm CL) for the 1971 and 1975 year-classes, respectively. Likewise, selectivity experiments by Blott et al. (1983) showed complete vulnerability of 19 mm CL *P. borealis* in a 32 mm stretch mesh trawl. Fox (1972) reported full recruitment at age 3 (≈18.0 mm CL) in stocks of *P. borealis* from Kodiak Island, Alaska, in which sampling was accomplished with trawls having a mesh size similar to those in the present study.

Table 5

Annual exploitation (μ), total (Z), fishing (F), and natural (M) mortality rates for the 1971 and 1975 year-classes.

	1971 year-class				1975 year-class[2]			
Age[1]	μ	Z	F	M	μ	Z	F	M
3.4/4.4					0.225	2.600	0.632	1.968
4.4/5.4					0.000	0.877	0.000	0.877
5.4/6.4	0.369	0.545	0.478	0.067	0.000	1.038	0.000	1.038
6.4/7.4	0.183	1.734	0.385	1.349				
7.4/8.4	0.121	3.813	0.472	3.341				

[1] Ages of year-classes correspond with years 1974–79 for 1971 and 1978–81 for 1975 (see Table 2).
[2] Fishery closed in 1979; thus, μ and F are both zero.

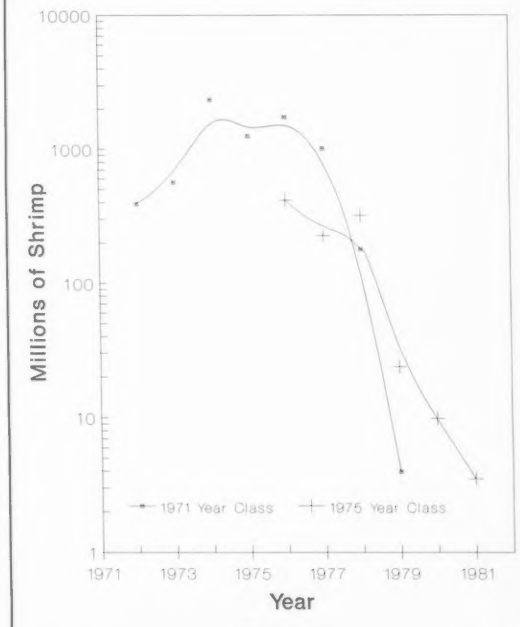

Figure 5

Catch curves (fitted by eye) of the 1971 and 1975 year-classes from Pavlof Bay survey data.

Mortality estimates

Total mortality estimates were based on year-class abundance after full recruitment to survey sampling (eq. 5; Table 5). The age of full recruitment to survey sampling was identified as 5.4 for the 1971 year-class and 3.4 for the 1975 year-class based on the visual inspection of the catch curve (Fig. 5). Since the commercial fishery was closed before the 1979 survey, total mortality rates estimated for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Table 5 also presents annual exploitation and fishing mortality rates estimated for both year-classes (from eq. 6). The 1971 year-class showed increasing natural mortality between ages 5.4 and 8.4, while fishing mortality remained relatively stable during this period.

Increasing total mortality with age for the 1971 year-class is attributed to increasing natural mortality since fishing mortality was constant. Apparent increases in natural mortality could also be caused by emigration of older individuals from the Pavlof Bay population, but this seems unlikely since it has been demonstrated that larger (older) shrimp are less active in diel vertical migration (Barr 1970) and would tend to be retained by the shallow entrance of Pavlof Bay. The observed higher natural mortality in this study may be the result of spawning stress or senescence since the 1971 year-class may have approached their maximum longevity. Predation by Pacific cod *Gadus macrocephalus* may have also contributed to the high mortality observed from ages 6.4 to 8.4 when cod catches increased from 10 to about 500 kg per nautical mile towed (Albers and Anderson 1985).

The 1975 year-class showed its highest calculated natural mortality between ages 3.4 and 4.4 (Table 5); however, these rates were subsequently lower. After closure of the fishery, the total mortality rates for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Albers and Anderson (1985) reported the significance of Pacific cod predation on *P. borealis* in Pavlof Bay. Pacific cod abundance peaked in 1979

and declined to about one-sixth of its former abundance by 1981. Lower observed natural mortality for the 1975 year-class beyond age 4.4 could be explained by decreasing cod predation.

Mortality estimates rely not only on the suitable definition of the year-class modes but also on the accuracy of biomass estimates (see eq. 2). Accuracy of biomass estimation is a function of the vulnerability, gear selectivity, and accessibility of shrimp in Pavlof Bay to the annual surveys. Knowledge of the life history of *P. borealis* were used to address these sources of variability in survey sampling. The late summer-fall period was chosen for sampling because *P. borealis* may be more vulnerable to capture due to the formation of mating and spawning aggregations. Small males and the larger females are not segregated, and even juvenile shrimp ≈6 mm CL can be found in these aggregations. Sampling was restricted to daylight hours to minimize the effect of diel vertical migration; thus, shrimp were more susceptible to capture by bottom trawling. Shrimp smaller than 18 mm CL are known to be less vulnerable to capture with the 32 mm mesh survey sampling gear. Sampling with smaller mesh (3.2 mm) in 1986 did indicate that more small shrimp could be captured, but small mesh sampling of the entire population was not deemed feasible due to increased sorting time.

Biomass estimates are considered conservative due to the lesser vulnerability of small shrimp. Likewise, larger/older shrimp may be able to escape capture by swimming out of the water column sampled by the survey trawl, leading to an overestimate of mortality. The high opening shrimp trawl used in this study (Wathne 1977) was designed to sample a substantial portion (3.8–4.4 m off bottom) of the water column. Biomass trends tend to refute avoidance of larger shrimp as a source of error.

Biomass estimates, while they may not be an absolute estimate of the population size, can represent an index. Sources of variability that could affect the validity of biomass estimates being used as an index were controlled. Survey timing, gear, methods, and even vessel type were the same throughout the survey series. Survey sampling methodology, while minimizing, may not always eliminate possible changes caused by availability of shrimp. *Pandalus borealis* may be more vulnerable to capture during mating and spawning because dense aggregations are probably beneficial for mating success. The exact timing of this event may vary from year to year. As an example, the 1972 and 1974 surveys both took place during the second week in September (Table 1). In 1972, about 60% of females were carrying eggs externally while only head roe (egg mass clearly visible under carapace) females were found in 1974. Changes in availability probably explain the dip in the catch curve for the 1971 year-class at age 4.4 and at 2.4 for the 1975 year-class (Fig. 5). These apparent changes in availability perhaps associated with some life-history stage or abiotic factor should be studied in order to improve both biomass and mortality estimates.

Table 6

Percent female of the 1971 and 1975 year-classes at age (years) from Pavlof Bay, Alaska, survey sample analysis.

	Age							
Year-class	1.4	2.4	3.4	4.4	5.4	6.4	7.4	8.4
1971	0	0	0	2	38	100	100	100
1975	0	0	0	100	100	100	—	—

Sex transformation

The rate of transformation from male to female was considerably different for the two dominant year-classes studied (Table 6). Some members of the 1971 year class initiated sex transformation during their fourth year; however, others transformed during either their fifth or sixth year. In contrast, all members of the 1975 year-class initiated and completed transformation during their fourth year. The age at and rate of sex change for a year-class also appear to be closely related to year-class size or overall population density. Charnov (1979, 1981) proposed a model in which high mortality rates lead to a shorter male phase. Charnov et al. (1978) also considered how natural selection might act to alter the sex ratio of Pandalid shrimp in response to environmental influences. I feel that accelerated sex transition observed for the 1975 year-class in this study was influenced by short-term phenomena and is evidence of the labile timing in sex change of this species. The occurrence in 1980 and again in 1984–86 of the smallest ovigerous females ever sampled (13.0 mm CL) is further evidence that accelerated sex reversal may be a possible mechanism by which northern shrimp attempt to increase reproductive capacity in the face of decreasing density (Table 1). Charnov and Anderson (1989) reported on an analysis of Pavlof Bay *P. borealis* that demonstrated the size of shrimp at the time of sex-transformation changes through time in relation to changes in the breeding size distribution.

Stock/recruit relationship and yield

While a compensatory relationship between lower population levels or density and the occurrence of early

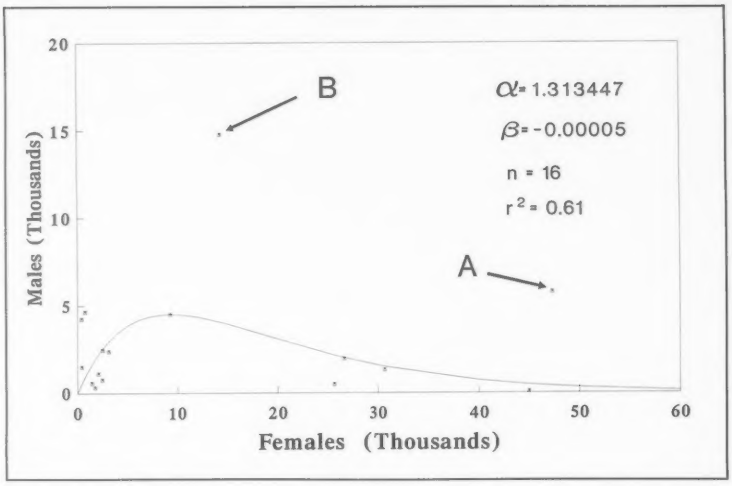

Figure 6
Spawner/recruit curve fit on female *Pandalus borealis* caught per kilometer as index of spawning biomass, and 1.4 year-olds (lagged one year) as recruit index, captured in Pavlof Bay shrimp surveys 1972–86. Points labeled A and B show effect of strong 1.4-age male year-classes of 1973 and 1975, respectively.

transformation of shrimp has been suggested in this study, the relationship between stock and recruitment appears to elude suitable definition. Using the average catch of females per tow as an index of spawning population and the catch rate of 1.4 year-old males as an index of recruits (lagged one year), a Ricker (1975) stock-to-recruit relationship was constructed (Fig. 6). While other combinations representing spawning and recruit biomass were tried, this combination gave the best fit to the recruitment function. Possible reasons for this combination rendering the best fit are that females are almost fully vulnerable to trawl capture and remain near the bottom during the fall survey period. On the other hand, while the 1.4 year-old males are not fully vulnerable to trawl capture, they do seem to represent a good relative index of incoming year-class strength. When dominant year-classes could be identified and followed through time, they were first identified as being relatively strong as 1.4 year-olds (Fig. 2). Since the 1.4 year-old mode is usually well separated from the remaining frequency distribution, weak as well as strong incoming year-classes could be quantified with the mode-separation technique.

Extreme fluctuations in the abundance of young year-classes make it difficult to devise management strategies. In some years, a relatively small spawning stock may give rise to a large year-class. The fit to the stock recruitment curve (Fig. 6) shows that the majority of the data points mostly conform to the fitted relationship. Outlying points labeled as A and B (A, 1973 year-class males (age 1.4) vs. brood females of 1972; and B, 1975 year-class males (age 1.4) vs. brood females of 1974) illustrate how relatively dominant 1.4 year-old male year-classes can push data points well outside the bounds of the curve (Fig. 6). The relative abundance of 1.4 year-old shrimp is probably a function of the variable survival of larvae and juveniles in response to environmental conditions rather than spawning biomass. The inadequacy of the fitted stock to recruit function to describe these important contributions to stock biomass means that other methods for defining management are needed. Therefore, strategies based on yield-per-recruit of dominant year-classes were examined.

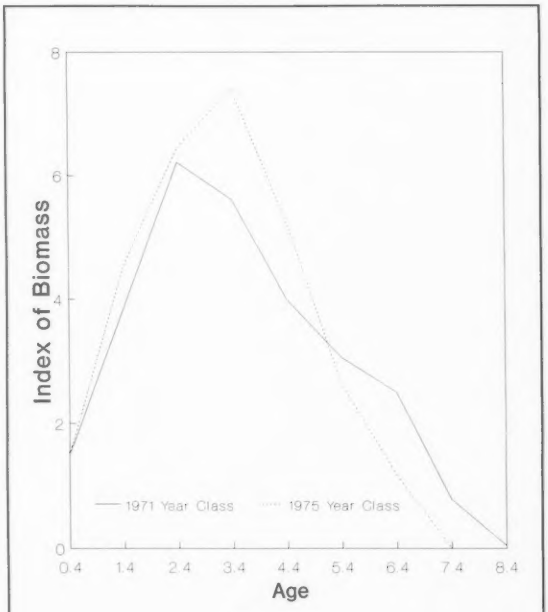

Figure 7
Biomass vector (in the absence of fishing) calculated using the technique of Paulik and Bayliff (1967) for the 1971 and 1975 year-classes.

Incorporating the growth and mortality estimates from this study into a Ricker yield model (Paulik and Bayliff 1967) indicated that maximum biomass, in the

absence of harvest, would be achieved at a relatively early age (Fig. 7) and small size. The maxima of biomass vectors were attained between age 2.4 (14.3 mm CL) and 3.4 (16.5 mm CL) for the 1971 year-class, and at age 3.4 (18.2 mm CL) for the 1975 year-class (Fig. 7). A management strategy based on maximizing the yield-per-recruit for the 1971 year-class would have resulted in the harvest of mostly male shrimp prior to their transformation to females. A similar finding was also reached by Abramson and Tomlinson (1972) in yield studies of *Pandalus jordani*. Harvesting more young shrimp may also lead to a possible lower economic return due to market resistance to small meats. Optimum management of Pandalid shrimp fisheries probably involves a trade-off between size-related economic return and larger yields from the harvest of young shrimp.

Conclusions

1 The bathymetric features of the Pavlof Bay region make it an ideal area for studying populations of *P. borealis*. The confining sills probably allow little immigration or emigration of shrimp. Thus dominant size modes, representing year-classes, could be followed through time in both the research survey and commercial data sets. It is necessary to rely on following dominant size modes to gain insight into population parameters owing to the problem of overlap with less dominant year-classes in the size-modal structure.

2 The Pavlof Bay population of *P. borealis* showed significant differences in year-class strength, with the 1971 year-class predominating during the study. Dominant year-classes are first detected when they are young (1.4 years old). Biotic or abiotic factors that control year-class strength have their greatest effect during the larval and juvenile stages.

3 There is evidence that growth may be inversely related to year-class strength. Since 1979, 1.4 year-old shrimp have averaged 13–15 mm CL rather than the 10–11 mm CL observed prior to 1979.

4 Age at sex transition was highly variable for the two dominant year-classes studied. The 1971 year-class showed transition over three years, while the 1975 year-class completed transformation in one year.

5 Total mortality rates of Pavlof Bay *P. borealis* are some of the highest reported for the species (Fréchette and Parsons 1983, Teigsmark 1983, Hopkins and Nilssen 1990) and are mostly a reflection of the high natural mortality rates. High natural mortality rates for the 1971 year-class are attributed to intense predation by Pacific cod (Albers and Anderson 1985). After the cod population subsided within the Bay, natural mortality, along with total mortality, declined.

6 Yield could have been maximized by harvesting more young (male) shrimp, since mortality rates were high for the year-classes studied.

Worldwide, other *P. borealis* fisheries have experienced similar cycles of high and low abundance (Balsiger 1981) that characterized the rise and fall of western Gulf of Alaska fisheries in the 1970s. The decline of shrimp in Pavlof Bay was probably inevitable, regardless of the presence of a fishery, since many adjacent areas lightly or seldom fished experienced similar population declines (Anderson and Gaffney 1977). These declines may be directly attributable to the demise of a single or series of strong year-classes. Little is known about the parameters controlling shrimp natality and its relationship to subsequent recruitment. This problem deserves study, along with the effects of predation (Albers and Anderson 1985) and ecological and environmental parameters (Nunes 1984). Continuing shrimp research surveys in Pavlof Bay may lead to understanding the dynamics and perhaps the mechanisms driving the cycle of low and high shrimp abundance in the western Gulf of Alaska.

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Bioenergetics and Growth of Northern Anchovy *Engraulis mordax*

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Abstract.–Changes in total body energy content of adult (total length ~9 cm, wet mass ~9 g) northern anchovy *Engraulis mordax* were estimated by sampling captive groups swimming at 8.7 and 21.1 cm/s for 12 hours daily. Anchovy were fed euphausiids at rations of 5 and 3.4% of fish wet mass per day (~54 and 37 cal · g fish wet mass^{-1} · day^{-1}, respectively). Gross energy conversion efficiency increased with ration levels and declined with swimming speed, ranging from 39% to 1%. Dry mass and lipid losses were estimated in fasting fish swimming at the same speeds. Energy losses were 17.6 and 28.2 cal · g fish wet mass^{-1} · day^{-1} at the slow and fast speeds, respectively. The proportion of food energy used for growth and maintenance metabolism was about 65%. A model derived for adult anchovy metabolism was consistent with observed growth and reproduction rates, and the few measurements of ration and swimming speed in nature.

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The incorporation of energy from food into growth and reproduction by northern anchovy *Engraulis mordax* has been roughly quantified. Prey abundance influences the rate of anchovy reproduction during subsequent years, according to time-series analysis (Smith and Eppley 1982). Abundant food probably results in more energy intake and storage. Energy available for growth and reproduction by northern anchovy in the wild has been estimated at 12.8% of energy intake, based on laboratory measurements of gross energy-conversion efficiency (Hunter and Leong 1981). At 12.8% efficiency, the daily ration needed for average growth and reproduction was estimated to be 4-5% of fish wet mass (Hunter and Leong 1981), which is towards the high end of the range of field estimates for engraulids (Blaxter and Hunter 1982). However, food intake and energy demands vary. An energy budget model could help explain and predict the effect of food availability on anchovy growth and reproduction.

Gross energy-conversion efficiency is the net energy remaining after food assimilation and metabolic losses divided by the total energy consumed as food. Thus, gross energy-conversion efficiency should tend to increase with ration and decrease with increased swimming activity. The impact of swimming activity on clupeoid metabolism has been described for Pacific sardine *Sardinops caerulea* (Lasker 1970), Atlantic menhaden *Brevoortia tyrannus* (Durbin et al. 1981), and Peruvian anchoveta *E. ringens* (Villavicencio 1981). Estimated metabolic rates of adult northern anchovy (S. Kaupp, R. Lasker, and R. Leong, a table of estimates obtained from J.R. Hunter, Southwest Fish. Sci. Cent., NMFS, NOAA, P.O. Box 271, La Jolla, CA 92037, unpubl. data) are about twice as high as those of its congener, *E. ringens*, at swimming speeds of about 1 body length/s. This difference is not small in relation to the overall energy budget of engraulids; therefore, better estimates of swimming metabolism are needed. The present study measures the energy expended for metabolism by northern anchovy at different swimming speeds, examines the effect of ration and metabolic rate on gross energy-conversion efficiency, and derives a model for adult anchovy metabolism.

Methods

The flume

Juvenile and adult northern anchovy ranging from 2 to 7 g wet mass were purchased from live-bait dealers in February 1984 and acclimated to laboratory conditions for 2–4 months prior to being transferred to an open flume for exercising the fish. Procedures for keeping live anchovy are described in Leong (1971) and Hunter and Leong (1981). Fish were fed 0.09 g Biomet trout pellets per fish per day until the study began.

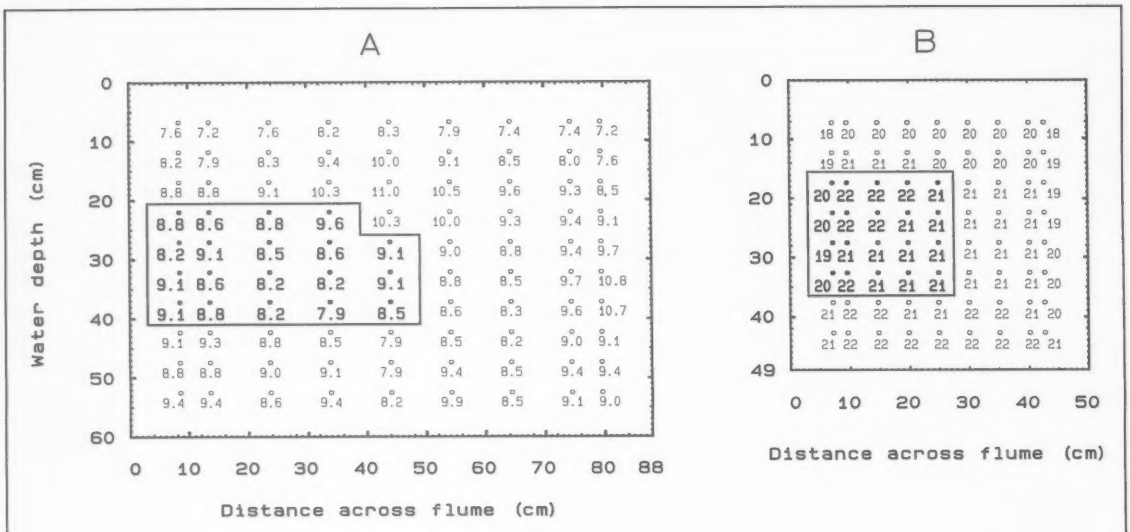

Figure 1

Cross-sections of two flume sections showing water speed (in cm/s). Outlined areas were habitually occupied by the fish, and the enclosed speed values (shown in bold) were averaged to obtain the swimming speed in the (A) slow and (B) fast sections.

The open flume was composed of two connected sections, the second section narrower and shallower than the first, resulting in a more rapid flow. The first section (the slow section) measured 244×88×60 cm (1290 L), and the second (the fast section) measured 244×50×49 cm (600 L). A 20 hp pump at the downstream end of the flume recirculated about 50 L/s of seawater through a feed pipe back to the upstream end of the flume. Water flowed through a tapered expansion section packed with gratings to even the flow. The whole flume was inside a 15,000 L tank. Fresh filtered seawater was added to the recirculating water in the flume at a rate of 20–30 L/minute. Temperature was maintained at 16.5–17.5°C.

Cross-sectional current profiles in each section were measured with a Marinco B-10 ducted impeller current meter. Baffles upstream from each section were adjusted to make the current profiles as uniform as possible, and gratings at the ends of each section confined the fish. Anchovy acclimated to the flume occupied habitual areas within the two sections (Fig. 1). The current measurements in these areas were averaged to estimate swimming speed. The pump was operated 12 hours daily during "daylight"; the photoperiod was 13L:10D with half-hour "dawn" and "dusk" periods.

Fish were anesthetized with quinaldine prior to transfer to the flume. During transfer, the fish were sorted and selected by size. A greater number were put in the larger (slow) flume section to make fish density similar in both sections. Initially 1600 and 1000 fish were put into the slow and fast sections, respectively. The 12-hour swimming regime was built up over 8–10 days and then maintained for 2–3 weeks for each treatment.

Treatments

Three levels of energy intake—high, zero, and low rations (in that order)—were imposed at two swimming speeds, making a total of six treatment combinations (Table 1). At each ration level, slow- and fast-speed treatments were applied concurrently in the two flume sections. The initial stock of fish was enough for the high- and zero-ration treatments. The flume was restocked for the low-ration treatments, but the number of laboratory-acclimated fish available was low (Table 1).

Starting 8–10 days before the treatments began, food type was changed to commercially obtained frozen euphausiids (species not identified). Anchovy were fed thawed euphausiids for 1 hour (high ration) or 0.5 hour (low ration) during the end of the daily swimming period. Food placed in 15 L containers of water above the flume flowed into perforated tubes (2.5 cm diameter, 0.6 cm perforations) stretched across the front of the two sections. Screens were temporarily inserted

Table 1

Summary of feeding levels in sequence of application, 12-hour enforced speeds, average fish mass, and estimated daily rations for the six treatments using the northern anchovy *Engraulis mordax*. N_C = initial number of fish in each flume section at the start of each treatment, N = total number killed for samples (number of samples in parentheses), and D = percentage of fish that died.

Treatments						Fish mass (g)			
Feeding level	Speed (cm/s)	N_C	N	D (%)	Wet mass of food per fish* (g/day)	Wet	Dry	Corrected daily ration** (% wet mass)	Ration energy (cal·g fish wet mass^{-1}·day^{-1})
High	8.7	1392	331 (4)	39	0.443	9.02	2.40	5.06	55.7
	21.1	674	184 (4)	49	0.442	9.83	2.57	4.73	52.0
0	8.7	469	291 (5)	8	0	8.86	2.68	0	0
	21.1	131	86 (3)	27	0	9.32	2.96	0	0
Low	8.7	416	298 (4)	16	0.227	6.82	1.92	3.42	37.6
	21.1	177	111 (2)	37	0.285	8.67	2.66	3.38	37.2

*Average from daily amounts dispensed and equations in Figure 2.
**Corrected for gastric evacuation (cf. Equation 4 in text).

to prevent food in one section from passing to the other. Uneaten food collected on the screens was weighed.

Rations were chosen to match the high ration (4–5%) estimated by Hunter and Leong (1981), and a lower ration (3%) in the middle of the range of field estimates (Blaxter and Hunter 1982). The zero ration was included so that metabolism could be estimated from the loss of body energy.

Preliminary estimates of rations were made from the net mass of food dispensed and the number of fish in each treatment (Table 1). Preliminary ration estimates were calibrated based on the amount of food in stomachs after feeding, corrected for gastric evacuation. To estimate the gastric evacuation rate, 15–24 fish were killed and stomach contents weighed once per hour for 7 hours on the seventh day of the first treatment.

Removing and counting fish

A sample of fish (Table 2)* was collected in one sweep of a large dipnet at the beginning and end of each treatment, and every 4–7 days during five of the six treatments. In the low-ration, fast-speed treatment there were enough fish only for the initial and final samples. At least 20 fish were planned for each sample, but the number of fish netted was sometimes lower, or much higher (Table 2)* because the sample was taken quickly to avoid disturbing the fish.

The standard length of sampled fish, their wet mass, and the wet mass of stomach contents were measured. A subset of about 20 fish from each sample and the combined stomach contents from 9 samples were dried for 6 days at 55°C, cooled in desiccators, and weighed.

A census was kept on the number of fish in each section of the flume based on rapid counts of the fish transferred to the flume, minus removals due to sampling and mortality. Dead fish were collected and measured each day. The initial counts were accurate to within 10% of the total number collected at the end of the treatments. A corrected census, figured from the total counts, was used in the final calculations.

Data analysis

Within each treatment, trends in sample means (i.e., length) or calculated values (i.e., kcal/fish) were expressed as slopes in relation to elapsed time by using linear regression (method of least squares). When only two samples were collected in a treatment, the difference over time was calculated. The significance of slopes, differences between initial and final sample means, and differences between values estimated from regression (i.e., log of dry mass) were evaluated with t-tests.

Apparent growth trends in some treatments were corrected to account for high mortality of fish smaller than the treatment mean. If there was no significant change in length (e.g., in zero-ration treatments), then no correction for mortality was made and length was assumed to be constant. An approximation of the bias in group mean length caused by mortality each day was calculated as the difference between the apparent mean length of the group each day (L_A) and the mean length calculated by including the dead fish collected that day,

*In the zero-ration treatments, sample size was the same as the number dried (Table 3).

Table 2

Increase in standard length (95% confidence intervals in parentheses) with time during the four feeding treatments and the correction for size-specific mortality. N_C = number of fish in each flume section before the first sample, N = sample size, N_S = stomach content sample size, and NA = not applicable.

Ration ($cal \cdot g^{-1} \cdot day^{-1}$)	Speed (cm/s)	Day	N_C	N	N_S	Mean length (mm)	Apparent growth in length	Mortality bias (mm/day)	Actual growth in length
High	Slow								
55.7	8.7	0	1392	101	0	88.1 (±1.2)			
		7	1160	168	157*	90.1			
		14	773	29	29	95.4			
		21	556	33	33	91.0 (±2.5)	0.202 (±0.569)	0.155	0.047
High	Fast								
52.0	21.1	0	674	99	0	88.9 (±1.1)			
		7	489	33	33	91.8			
		14	327	22	22	95.4			
		21	187	30	30	94.1 (±2.5)	0.277 (±0.324)	0.244	0.033
Low	Slow								
37.6	8.7	0	416	75	24	84.4 (±1.1)			
		7	319	78	24	84.1			
		14	212	70	24	85.5			
		20	126	75	24	86.0 (±1.3)	0.092 (±0.099)	0.023	0.069
Low	Fast								
37.2	21.1	0	177	52	24	93.9 (±1.7)			
		16	59	59	24	92.9 (±1.7)	−0.063	NA	0

*Total of 8 samples (Fig. 3) collected 0–7 hours after feeding (N_S = 23, 21, 19, 16, 24, 15, 15, and 24, respectively).

Daily bias =

$$L_A - \left[\frac{(L_A N_C) + (L_M N_M)}{N_C + N_M} \right] \text{mm/day}, \qquad (1)$$

where N_C was the number of fish in the treatment group at the end of each day, N_M was the number of dead fish that day, and L_M was the mean standard length of the dead fish that day. The L_A was calculated from a regression of sample mean lengths on elapsed time over the course of the treatment. The slope of this regression (L_A on elapsed time) was the apparent growth (Table 2), which was corrected by the average of the daily biases to estimate the actual increase in fish length.

Fish mass was estimated from corrected length using log–log regressions of dry mass on standard length for each sample. The regression estimate for each sample was calculated by assuming that length increased at the corrected rate for that treatment.

From each sample, a subset of four fish, chosen to best match the estimated length and dry mass of the sample, was analyzed for fat content by using Soxhlet extraction with chloroform-methanol (2:1). Fat content of food removed from stomachs was also measured. Total energy content of fish and food was estimated from published values (Brett and Groves 1979, Hunter and Leong 1981) for heat of combustion. The rate of energy loss or gain in each treatment was calculated as the regression slope of fish energy content in each sample versus elapsed time.

Results

Rations

Anchovy stomach contents from 12 samples (Table 2) were weighed immediately after feeding. The average amount of food in the stomachs was less than (but correlated with) the net amount of food that was dispensed per fish (Fig. 2). The difference was too large to be due to the rate of gastric evacuation. A portion of the food passed through gaps in the bottom of the flume sections and into the surrounding tank. Recirculation of this food was prevented by screens. Regressions of stomach contents on food dispensed (Fig. 2) suggested that a greater proportion of the food dispensed was eaten in the high-ration, fast-speed treatment than in the other treatments. Although the regressions were not significantly different, they were used to estimate stomach contents separately for each speed on days when stomach contents were not sampled. The average of the resulting daily estimates was calculated for each treatment (Table 1).

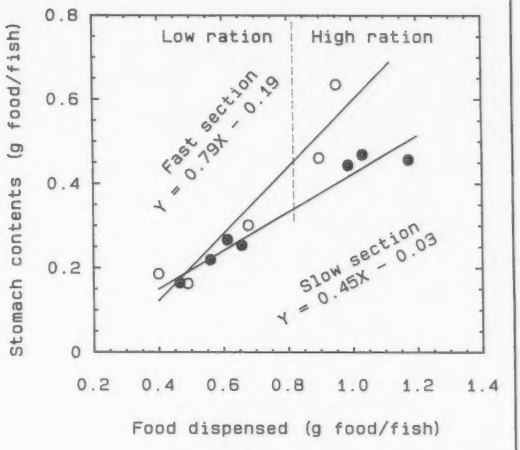

Figure 2

Relationship between the net amount of food dispensed per anchovy and stomach contents (wet mass of food/fish) after feeding in the slow (filled circles) and fast sections (open circles) of the flume. Each point is the mean for a sample of N_S fish (Table 2).

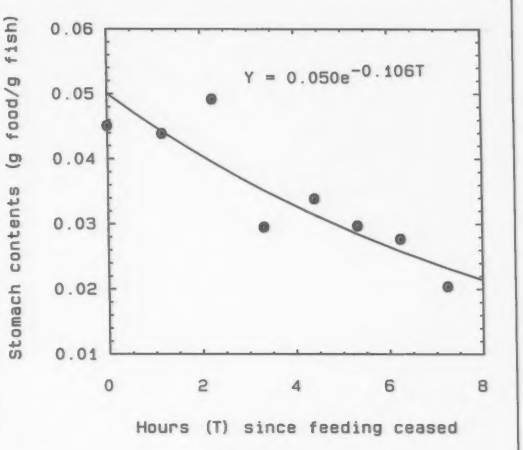

Figure 3

Gastric evacuation rates of northern anchovy fed euphausiids (food wet mass/g wet mass fish). Each point is the mean for a sample of N_S fish (Table 2).

Evacuation of the food from the stomach was slow (Fig. 3). The absence of an immediate decline in stomach contents after feeding suggested a gastric pause or coprophagy, although this result may be due to sampling errors. The following regression (using a semilog transformation) of mean stomach contents (Y in grams food/gram fish) versus elapsed time (T in hours after feeding stopped) describes the data from eight hourly samples (Table 2, Fig. 3):

$$\log_e Y = -2.995 - 0.106\,T \quad (N\ 8,\ r^2\ 0.81). \quad (2)$$

Taking the antilog

$$Y = 0.05\ e^{-0.106\,T}\ \text{g food / g fish}, \quad (3)$$

the actual amount of food consumed (C_T) between the initiation and cessation of feeding was estimated (Elliott and Persson 1978) as

$$C_T = \frac{[S_T - (S_0\ e^{-dT})]\ rT}{1 - e^{-dT}}\ \text{g food}, \quad (4)$$

where S_T was the amount of food found in stomachs at the cessation of feeding, and d = 0.106 (from Equation 3). No food was in the stomachs at the initiation of feeding (S_0 = 0). For 1 hour of feeding, C_T equaled 1.054 S_T, and for 0.5 hour of feeding, C_T equaled 1.027 S_T. Thus, only a slight correction of mean stomach content estimates was needed to calculate the rations (Table 1).

The water content of food (euphausiids) averaged 78.4% (*N* 9, SD 1.7%); therefore, dry mass averaged 21.6% of wet mass. The fat content of the food averaged 21.8% of dry mass (*N* 3, SD 3.6). S. Kaupp (NMFS Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92037, pers. commun., March 1984) found that the average protein content of euphausiids (species not identified) was 43.5% of dry mass (*N* 25, SD 0.20). The remaining dry mass (24.7%) was estimated to consist of ash and chitin in roughly equal amounts, since Lasker (1966) found that molts and ash each made up about 10% of dry mass in *Euphausia pacifica*. Assuming 9.2 kcal/g for fat, 5.65 kcal/g for protein, and 4.1 kcal/g for carbohydrate (Brett and Groves 1979), the total caloric content of the food was

$$\left[\frac{21.8}{100}\ 9.2\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{43.5}{100}\ 5.65\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{12.4}{100}\ 4.1\ \frac{\text{kcal}}{\text{g dry}}\right] = 5.09\ \frac{\text{kcal}}{\text{g dry food}}$$

and

$$\left[5.09\ \frac{\text{kcal}}{\text{g dry food}}\right]\left[\frac{21.6\text{g dry}}{100\text{g wet food}}\right] = 1.1\ \frac{\text{kcal}}{\text{g wet food}}.$$

Growth in length

Final mean length was significantly higher than the initial mean length in all feeding treatments except the low-ration, fast-speed treatment (t-test, $P \leq 0.05$; Table 2). However, the slopes of the regressions describing the apparent rates of growth (in length) were not significantly different from zero, because of the variation not explained by growth or selective mortality. The fish schooling in the flume may have sorted themselves by size so that the dipnet frequently caught a sample containing larger- or smaller-than-average fish. The coefficient of variation of length in each sample ranged from 5 to 7%. The low number of samples would make this an important source of error.

Table 3

Regressions of the natural log of dry mass ($\log_e$ Y) on the log of standard length ($\log_e$ X) estimated from actual growth (cf. Table 2), and measures of fat content (N 4) used to estimate dry mass, total energy, caloric growth, and energy loss during the six treatments. Estimates in brackets assume no increase in length; 95% confidence limits in parentheses. N = number of fish dried.

Treatment	Day	N	Regression equation	Length (mm)	Log of dry mass from regression	Dry mass (g)	Fat content (%)	Total energy (kcal)
High ration, slow speed								
	0	25	$\log_e Y = 3.861 \log_e X - 16.664$	89.04	0.668 (±0.091)	1.95	36.7	11.70
	7	32	$\log_e Y = 5.241 \log_e X - 22.814$	89.36	0.732	2.08	39.8	12.87
	14	19	$\log_e Y = 4.679 \log_e X - 20.333$	89.69	0.705	2.02	40.9	12.61
	21	23	$\log_e Y = 4.605 \log_e X - 19.784$	90.02	0.939 (±0.059)	2.56	43.9	16.30
				[89.04]	[0.888 (±0.059)]	[2.43]		
High ration, fast speed								
	0	24	$\log_e Y = 5.524 \log_e X - 23.943$	88.68	0.832 (±0.078)	2.30	41.7	14.39
	7	23	$\log_e Y = 3.893 \log_e X - 16.587$	88.91	0.883	2.42	43.7	15.38
	14	12	$\log_e Y = 5.193 \log_e X - 22.467$	89.14	0.851	2.34	43.8	14.89
	21	20	$\log_e Y = 4.574 \log_e X - 19.611$	89.37	0.939 (±0.056)	2.56	44.8	16.42
				[88.68]	[0.903 (±0.060)]	[2.47]		
Low ration, slow speed								
	0	24	$\log_e Y = 4.515 \log_e X - 19.493$	84.06	0.515 (±0.062)	1.67	38.4	10.16
	7	24	$\log_e Y = 4.839 \log_e X - 20.856$	84.54	0.616	1.85	41.1	11.51
	14	24	$\log_e Y = 5.485 \log_e X - 23.712$	85.02	0.657	1.93	39.2	11.83
	20	24	$\log_e Y = 5.539 \log_e X - 24.050$	85.44	0.586 (±0.066)	1.80	40.5	11.15
				[84.06]	[0.496 (±0.067)]	[1.64]		
Low ration, fast speed								
	0	41	$\log_e Y = 3.352 \log_e X - 14.245$	93.4	0.963 (±0.032)	2.62	46.4	17.02
	16	49	$\log_e Y = 3.906 \log_e X - 16.733$	[93.4]	[0.988 (±0.047)]	*[2.62]	46.8	17.07
No food, slow speed								
	0	19	$\log_e Y = 4.587 \log_e X - 19.767$	92.52	1.000 (±0.076)	2.72	46.2	17.38
	4	24	$\log_e Y = 4.975 \log_e X - 21.499$	do.	1.025	2.79	47.6	17.96
	8	23	$\log_e Y = 5.293 \log_e X - 23.041$	do.	0.923	2.52	44.2	15.76
	12	21	$\log_e Y = 4.838 \log_e X - 21.016$	do.	0.888	2.43	45.1	15.36
	16	24	$\log_e Y = 5.611 \log_e X - 24.716$	[92.52]	[0.914 (±0.063)]	[2.49]	43.1	15.56
No food, fast speed								
	0	21	$\log_e Y = 3.553 \log_e X - 14.947$	93.48	1.176 (±0.064)	3.24	45.2	20.97
	6	23	$\log_e Y = 4.903 \log_e X - 21.210$	do.	1.039	2.83	46.8	18.57
	12	42	$\log_e Y = 3.542 \log_e X - 15.066$	[93.48]	[1.007 (±0.051)]	[2.74]	46.1	17.82

*Assumed no change in dry mass since the difference was not significant.

Estimates of actual growth (in length), as corrected for mortality (Table 2), appeared similar to those for 1- to 2-year-old anchovy in nature based on otolith increments (Spratt 1975), but were lower than those measured by Hunter and Leong (1981) in the laboratory. No increase in length was indicated during the low-ration, fast-speed treatment, so no correction was made for mortality. The most rapid length increase (0.069 mm/day) was estimated for the group with the smallest mean size (Table 2). This group underwent the low-ration, slow-speed treatment yet appeared to have a faster rate of growth (in length) than did the high-ration, slow-speed group. This might suggest that the increase in length was size-dependent and somewhat independent of the net energy surplus.

Mortality was highest during the high-ration treatments and lowest in the low-ration and fasting treatments, especially at slow speed (Table 1). Fish bumped into the gratings between flume sections during feeding, which may have led to a high rate of injuries resulting in death. The size bias in mortality might have resulted from large fish being less often injured by the gratings. However, the treatment with the smallest sized fish (low-ration, slow-speed) had one of the lowest mortality rates.

Dry mass

Estimates of fish dry mass for each sample were obtained from mass-on-length regressions (Table 3) by using length estimates corrected for mortality in three feeding treatments (Table 2) and assuming no length change in the other treatments. In all but one case, the final dry mass estimates were significantly greater (high- and low-ration treatments) or lower (zero-ration treatments) than the initial estimates (t-test, $P \leq 0.05$). In the zero-ration treatments, the loss of dry mass was more than twice as rapid in the fast-speed treatments as it was in the slow-speed treatments (Table 3). Dry mass increased about four times more rapidly during the high-ration treatments than during the low-ration treatments, and dry mass increased more than twice as rapidly during slow-speed treatments as during fast-speed treatments at both rations. Dry mass did not change significantly between the initial and final estimates when fish were fed the low ration and swam at the fast speed, so growth was assumed to be zero (Table 3).

In three feeding treatments (Table 3) the increases in mass were dependent on estimated increases in length. Although realistic, the corrected length increases (Table 2) may not have been accurate. Therefore, conservative estimates of mass increases in the feeding treatments were calculated by assuming that there was no increase in length (Table 3). A significant length-specific increase over initial dry mass was found in the slow-speed, high-ration treatment.

Caloric growth and gross conversion efficiency

Fat content (Table 3) increased substantially during the high-ration treatments, wherein about 70% of the increase in dry mass was fat. Fat increased about twice as much in the high-ration, slow-speed treatment as in the high-ration, fast-speed treatment. No strong trends in percent fat were found in the low-ration treatments.

The average percent fat of each sample was used to calculate mass of fat and fat-free dry mass per fish. Then the total fish energy content for each sample was calculated (Table 3) by assuming heat of combustion values equal to 29 kcal/g for fat-free dry mass and 9.227 kcal/g for fat (Hunter and Leong 1981).

The trends in total energy content from all of the treatments (Fig. 4) were consistent with a simple energy budget in which more food energy taken in (R), or less energy required for metabolism (Q), results in more energy available for reproduction (S), growth (G), and fat storage (F):

$$R = Q + X + I + S + G + F \text{ cal.} \qquad (5)$$

Components of the energy budget that were not individually estimated were excretion (X) and digestive losses (I). No spawning occurred during the experiments, although gonad mass changed. In the following analyses, changes in gonad and somatic mass were combined as overall growth (B) and fat storage (F). Metabolism was separated into maintenance metabolism (Q_M) and the metabolism associated with extracting usable energy from food (SDA). Ninety percent of the energy losses during starvation were assumed to be respired (Q_M), with excretion accounting for the remainder. This is consistent with estimates of endogenous excretion given by Durbin and Durbin (1981, 1983). The "metabolizable fraction" of fasting energy losses has been assumed to be as little as 80% (Brett 1973) for energy derived from body protein. In the present study, about one-third to one-half of the calories lost during fasting were derived from protein.

Energy losses during fasting were greatest during the fast-speed treatment (28.2 cal · g fish wet mass^{-1} · day^{-1})** and lowest during the slow-speed treatment (17.6 cal · g^{-1} · day^{-1}, Fig. 4). Growth (in cal · g^{-1} · day^{-1}) was greater at both speeds when rations (R) were high than when they were low (Fig. 4). At both

** Hereafter the unit of mass (g^{-1}) refers to fish wet mass.

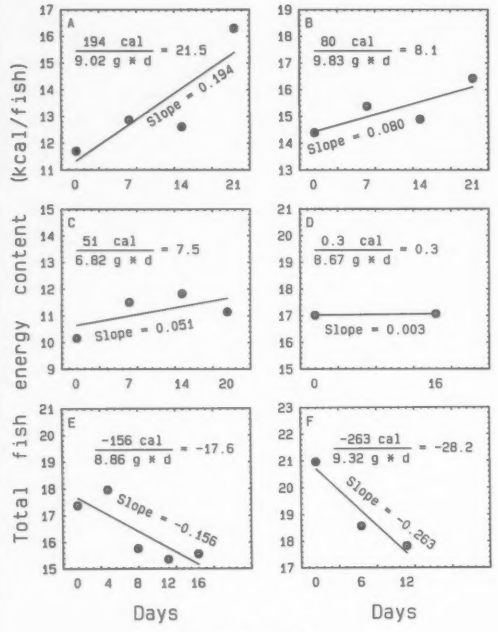
A
194 cal / 9.02 g * d = 21.5
Slope = 0.194
B
80 cal / 9.83 g * d = 8.1
Slope = 0.080
C
51 cal / 6.82 g * d = 7.5
Slope = 0.051
D
0.3 cal / 8.67 g * d = 0.3
Slope = 0.003
E
-156 cal / 8.86 g * d = -17.6
Slope = -0.156
F
-263 cal / 9.32 g * d = -28.2
Slope = -0.263
Total fish energy content (kcal/fish)
Days
Days

Figure 4

Estimated rates of changes in fish energy content. Slopes were converted into mass-specific rates of caloric growth at the high-ration level for (A) slow-swimming and (B) fast-swimming speeds and at the low-ration level for (C) slow-swimming and (D) fast-swimming speeds. Negative slopes from the zero-ration treatments were converted into mass-specific rates of energy loss for (E) slow-swimming and (F) fast-swimming speeds.

feeding levels, caloric growth was greater in the slow-speed than in the fast-speed treatments. In each treatment, energy utilization (in cal $\cdot g^{-1} \cdot day^{-1}$) not accounted for by maintenance metabolism (Q_M) and caloric growth (B+F) was a relatively constant fraction of the energy consumed:

	Ration (R)	–	Growth (B+F)	–	Maintenance (Q_M)	=	Excretion (X)	+	Digestive losses (I)	+	SDA
High ration, slow speed:	55.7	–	21.5	–	0.9(17.6)	=			20.1		= 0.36R
High ration, fast speed:	52.0	–	8.1	–	0.9(28.2)	=			18.5		= 0.36R
Low ration, slow speed:	37.6	–	7.5	–	0.9(17.6)	=			14.3		= 0.38R
Low ration, fast speed:	37.2	–	0.3	–	0.9(28.2)	=			11.5		= 0.31R

Mean 0.35R

About 35% of the food energy was lost through excretion (X), digestive losses (I), and SDA, so the energy budget Equation (5) may be simplified as

$$R = (B + F + Q_M) / 0.65 \text{ cal} \cdot g^{-1} \cdot day^{-1}. \quad (6)$$

Observed gross conversion efficiency (K) was calculated by dividing caloric growth (B + F) by ration (R). Gross conversion efficiency predicted by the energy budget approximation (Equation 6) was

$$K = \frac{R - (0.35\ R) - Q}{R} \text{ (dimensionless).} \quad (7)$$

The model closely matched the observed gross conversion efficiencies:

	Gross conversion efficiency (%)	
	Observed	Equation (7)
High ration, slow speed:	39	37
High ration, fast speed:	16	16
Low ration, slow speed:	20	23
Low ration, fast speed:	1	–3

These results indicate that a simple energy budget model, assuming a loss of 35% of the food energy due to X, I, and SDA, explains increased growth with increased ration and decreased growth with increased activity.

Discussion

Gross conversion efficiencies

The energy budget approximation (Equation 7) implies that gross conversion efficiency is reduced by low ration and high activity. This was supported by the lower

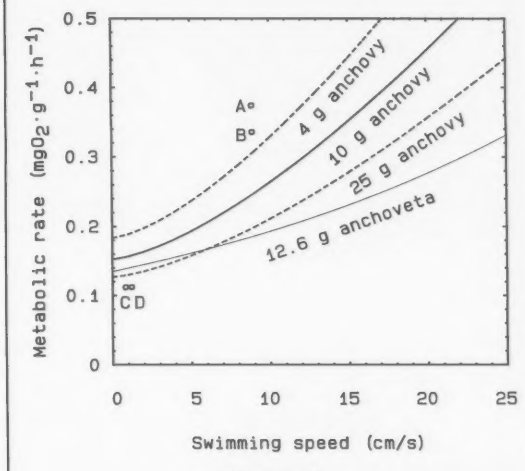

Figure 5

Comparison of other engraulid metabolic rate estimates with model predictions for 4, 10, and 25 g northern anchovy at 17°C. The anchoveta curve is from Villavicencio (1981, temp. 17°C). Respiration rates of (A) actively swimming 10 g northern anchovy at 15°C and, based on energy losses during zero-ration treatments, (B) exercised 16.9–17.8 g fish at 21°C, (C) non-exercised 13.5–16.9 g fish at 18°C, and (D) non-exercised 12.3 g fish at 15.2°C as measured by Kaupp et al. (unpubl. data).

K values in treatment combinations with low ration or high speed compared with the high-ration, slow-speed treatment. Contrarily, K values in the high-ration, slow-speed treatment were much higher than the 12.8% reported by Hunter and Leong (1981) for northern anchovy even though the fish in the present study were exercised and fed smaller rations. Hunter and Leong (1981) fed fish 124 cal · g^{-1} · day^{-1} of semi-dry, pelleted trout food (the caloric equivalent of a ration of 16% of wet body mass/day in copepods). At very high rations, the proportion of food energy lost to X, I, and SDA may increase (Paloheimo and Dickie 1966, Brett 1979, Brett and Groves 1979), causing K to decline.

The euphausiids used for food and the rations (Table 1) in the present study were similar to the zooplankton rations of 1.4–4.9% observed in nature (Blaxter and Hunter 1982). So, although X, I, and SDA vary with food composition (Elliott 1976b, Brett and Groves 1979, Tandler and Beamish 1979 and 1980) and may increase at ration levels higher than those in nature, the energy budget generalizations in Equations (6) and (7) should be applicable to adult anchovy in the wild.

The observed range of gross conversion efficiencies (1–39%) extended higher than the range reported for clupeoids (7–13.5%, Takahashi and Hatanaka 1960, De Silva and Balbontin 1974, Hunter and Leong 1981, Blaxter and Hunter 1982). However, gross conversion efficiencies this high are found in many juvenile fishes (60% Hatanaka and Takahashi 1956, 34% Elliott 1976a, 10–25% Brett and Groves 1979). The importance of different results in such studies is difficult to judge, because of differences in the assumptions, expressions (percentages of mass or energy), experimental conditions (size, maturity, temperature, activity), and the rarity of error estimates.

A model for adult anchovy metabolism

A model for anchovy metabolism was derived by using the estimates from the present study, data on closely related species, and general principles relating swimming speed and metabolism to fish size. The model required estimates of (1) standard metabolism, (2) swimming metabolism, (3) the effect of fish size on standard and swimming metabolism, and (4) the effect of temperature. These estimates are provided in the following sections.

Standard metabolism Standard metabolism was estimated by extrapolating to zero swimming speed from the rates estimated at two speeds. An exponential relationship (Brett 1964) was assumed,

$$Q_M = ae^{bV} \text{ cal} \cdot g^{-1} \cdot day^{-1}, \quad (8)$$

where the metabolic rate exclusive of SDA (Q_M) consists of standard metabolism (Q_0 = a) increased by a factor (e^{bV}) for the cost of swimming, where V is swimming speed. The energy losses measured in the present study resulted from fish exercising half the time and resting half the time, so

$$Q_M = [0.5\ (ae^{bV})] + [0.5\ (a)] \text{ cal} \cdot g^{-1} \cdot day^{-1}. \quad (9)$$

The metabolic rate estimates ($Q_M = 0.9 \times 17.6 = 15.8$, and $0.9 \times 28.2 = 25.4$ cal · g^{-1} · day^{-1}) from the two exercise levels (V = 8.7 and 21.1 cm/s, respectively) were substituted for Q_M and V in Equation (9). The resulting simultaneous equations were solved, and Q_0 was calculated to be 12.1 cal · g^{-1} · day^{-1} at V = 0. Assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975), the standard metabolic rate was 0.156 mg O_2 · g^{-1} · h^{-1}. Assuming the same metabolizable fraction (0.9) and oxycalorific equivalent, energy losses of 9.7 cal · g^{-1} · day^{-1} at the lowest activity levels measured by S. Kaupp et al. (unpubl. data,) amounted to 0.112 mg O_2 · g^{-1} · h^{-1}. The standard metabolism of 12.6 g anchoveta at 17°C (Villavicencio 1981) was 0.135 mg O_2 · g^{-1} · h^{-1}. These values (Fig. 5)

were similar to the estimate of Q_M in the present study.

Swimming metabolism Standard metabolism (Q_0 = 12.1 $cal \cdot g^{-1} \cdot day^{-1}$) subtracted from the Q_M estimates for fish at the two speeds left 3.7 and 13.3 $cal \cdot g^{-1} \cdot day^{-1}$, respectively, for the metabolic cost of swimming (Q_V) for 12 hours a day at 8.7 and 21.1 cm/s. On an hourly basis, Q_V amounted to 0.308 and 1.11 $cal \cdot g^{-1} \cdot h^{-1}$, respectively. A linear fit to log-transformed estimates of Q_V versus log-transformed V indicated that

$$Q_V = (0.0137\ V^{1.44})\ cal \cdot g^{-1} \cdot h^{-1}. \quad (10)$$

For extrapolating beyond the range of measurements, a power function makes a good model for swimming metabolism, because mechanical principles and empirical evidence (Ware 1978, Wu and Yates 1978) indicate that thrust and drag in swimming fish are power functions of speed.

Effect of fish size Fish size was not manipulated in the present study, so size effects could not be quantified from the results. However, reviews (Winberg 1956, Brett and Groves 1979) of results from a large number of studies have led to the generalization that the mass exponent of standard metabolism in fishes is close to 0.8. The corresponding mass-specific exponent (−0.2) combined with the estimate of Q_0 from the present study results in this model,

$$Q_0 = 18.8\ M^{-0.2}\ cal \cdot g^{-1} \cdot day^{-1}$$

$$= 0.783\ M^{-0.2}\ cal \cdot g^{-1} \cdot h^{-1}, \quad (11)$$

where M is anchovy wet mass (~9g in the present study).

The effect of fish size on the cost of swimming can be modeled by expressing speed relative to length so that the cost of swimming at the normalized speed is the same for any size of fish. The cost of swimming in sockeye salmon *Oncorhynchus nerka*, obtained by subtracting standard metabolism from total metabolism of 8–54 cm salmon swimming at speeds of 13–143 cm/s (Brett 1965), can be accurately described by a power function of the Reynolds number (Wu and Yates 1978). The Reynolds number combines fish length, speed, and kinematic viscosity. A similar way of expressing this relationship, which matches Brett's (1965) results (at 15°C) extremely closely, is

$$Q_V = 8.7934 \left[\frac{V}{L^{0.64}}\right]^{1.71} mg\ O_2 \cdot kg^{-1} \cdot h^{-1}. \quad (12)$$

Thus, for different sizes of sockeye salmon, the cost of swimming is the same when speed (V) divided by fish length (L in cm) to the 0.64 power is the same. This relationship is also reflected in length exponents (0.5–0.7) for endurance speed in fishes (Bainbridge 1962, Hunter 1971). Note that dividing V by L (body lengths/second) does not normalize speed with respect to swimming cost or endurance. For anchovy, the present study assumed that the length exponent for normalized speed was 0.6. Then, from Equation (10)

$$Q_V = 0.095 \left[\frac{V}{L^{0.6}}\right]^{1.44} cal \cdot g^{-1} \cdot h^{-1}, \quad (13)$$

and the cost of swimming in anchovy can be estimated for any size and swimming speed.

Effect of temperature Anchovy metabolic rates were estimated at only one temperature (17°C) in the present study, but the effect of temperature on engraulid anchovy metabolism was estimated for Peruvian anchoveta (Villavicencio 1981) at 14–20°C. These data indicated an increase of 78% in total respiration rate over a change of 6°C. Applying this intensity of temperature effect to the model would amount to

$$Q' = 2.046\ Q\ e^{0.0959\ T}\ (\text{in any units}), \quad (14)$$

where Q is the metabolic rate (in any units) at 17°C, and T is the ambient temperature (°C). However, short-term temperature acclimation periods in the laboratory (Villavicencio 1981) may result in greater metabolic rate changes than in the long term in nature. Estimates from Equation (14) should be viewed skeptically, until better estimates of the effect of temperature on anchovy metabolism can be found.

Evaluation of the model

Estimates of maintenance metabolism ($Q_M = Q_0 + Q_V$) from the model (Equations 11 and 13) for 4, 10, and 25g northern anchovy at 17°C were compared with other data on engraulids (Fig. 5), assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975). Oxygen consumption of northern anchovy swimming at about 9 cm/s in an annular respirometer was 0.38 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (Kaupp et al. unpubl. data). The rate of energy loss in fasting northern anchovy swimming in a flume at about 9 cm/s was 29.3 $cal \cdot g^{-1} \cdot day^{-1}$ or 0.34 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (Kaupp et al. unpubl. data, energy loss multiplied by 0.9, the metabolizable fraction). These data were about twice as high as the tunnel respirometry data on anchoveta (Villavicencio 1981) swimming at 9 cm/s (Fig. 5). The model

predicts metabolic rates in the middle of this range, indicating that it may provide reasonable estimates for engraulid metabolism.

To use the model to estimate ration, the energy required for standard metabolism (Equation 11) and the cost of swimming (Equation 13 converted to $cal \cdot g^{-1} \cdot day^{-1}$) plus the energy needed for growth or reproduction, are multiplied by 1/0.65 (from Equation 6) to account for X, I, and SDA. The result is the daily food energy requirement. Similarly, 65% of food energy minus standard and swimming metabolism gives the surplus available for growth and reproduction at that level of food intake and activity.

Hunter and Leong (1981) estimated the food energy requirements of 1-year-old anchovy (wet mass 10.3 g, length 10.3 cm) at 33.8 $cal \cdot g^{-1} \cdot day^{-1}$ (copepods at 4% of wet mass/day). According to the model in the present study, X, I, and SDA remove 11.8 $cal \cdot g^{-1} \cdot day^{-1}$, and standard metabolism (Equation 11) is 11.8 $cal \cdot g^{-1} \cdot day^{-1}$. Supposing 1-year-old anchovy swim at 12 cm/s for 12 hours each day, this costs 0.45 $cal \cdot g^{-1} \cdot h^{-1}$ (Equation 13), or 5.4 cal/g. If they swim at 2 cm/s for the other 12 hours, this costs another 0.4 cal/g, making the total swimming cost 5.8 $cal \cdot g^{-1} \cdot day^{-1}$. Subtracting all these costs from the ration energy leaves 4.4 $cal \cdot g^{-1} \cdot day^{-1}$, which Hunter and Leong (1981) estimated to be enough for normal growth plus 20 spawnings per year.

Is this level of swimming activity realistic? Using sonar tracking and Doppler shift analysis, Holliday (1977) measured a relatively uniform swimming speed averaging 45 cm/s over a 40-minute interval for what were thought to be northern anchovy about 14 cm long (25 g). To swim for 12 hours a day at this speed, while maintaining normal growth and spawning 20 times per year, 3-year-old anchovy (Hunter and Leong 1981) would require a ration of 7.7% of body weight per day. However, 3 hours a day at this speed, with the rest of the day at 3 cm/s, would allow for the same growth and reproduction on a ration of only 4%.

It appears that anchovy growth rates in nature and the estimate of spawning 20 times per year (Hunter and Leong 1981) are consistent with the current study's model predictions for anchovy swimming at speeds and consuming rations similar to those observed in nature. Three aspects of the model were determined by experiment: (1) A constant proportion of food energy is available for metabolism and growth, (2) metabolism increases with swimming speed, and (3) gross energy conversion efficiency is a function of ration level and activity. The model should be useful in estimating the effect of changing food abundance on spawning frequency and growth, particularly as more measurements of activity become available.

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Effects of Temperature on Early-life-history Stages of California Halibut *Paralichthys californicus*

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Abstract.–Laboratory experiments were conducted to determine how growth and survival of early-life-history stages of California halibut *Paralichthys californicus* are influenced by temperature, and how optimal temperature ranges may change with ontogeny. As halibut developed from eggs to juveniles, highest survival occurred at increasingly higher temperature ranges. Within tolerance limits, growth and development rates of all early-life-history stages were directly proportional to temperature. Eggs hatched successfully at 12, 16, and 20°C; at 8 and 24°C they died prior to embryo formation. Larval survival 17 days after hatching was 23–46% at 16, 20, and 24°C, but almost all larvae died at 12°C after an initial period of high survival. At 8°C, larval development ceased at the early yolksac stage. Survival of 3-month-old juvenile halibut was significantly greater at 20, 24, and 28°C (57–76%) than at 16°C (31%). Temperature also affected settlement rate; when the temperature of 1-month-old larvae was raised from 16°C to 20°C, settlement occurred about a week sooner than settlement of larvae remaining at 16°C. Tolerance ranges of halibut early-life-history stages determined in the laboratory approximate temperatures encountered by halibut in the field; high densities of newly-settled halibut larvae and juveniles have been collected in shallow areas of bays where temperatures are often higher than the open ocean inhabited by young larvae. These warmer inshore nursery grounds could enhance growth and survival of halibut juveniles.

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The California halibut *Paralichthys californicus* (family: Paralichthyidae) is important to commercial and recreational fishermen in central and southern California. Adult halibut spawn in nearshore waters (Frey 1971, Lavenberg et al. 1986) and eggs hatch in about 2 days at 16°C (Gadomski et al. 1990). Lavenberg et al. (1986) collected halibut larvae year-round within the 75 m contour of the Southern California Bight, with greatest abundance during winter and spring. When larvae are about 1-month-old and 8 mm standard length, they metamorphose and settle to the bottom (Allen 1988, Gadomski et al. 1990). Although spawning has not been observed in bays and estuaries, high densities of newly-settled halibut larvae and juveniles have been collected in these areas, often in waters as shallow as one meter (Allen 1988, Kramer 1990). It is not known at what stage of development inshore movement occurs, and whether the mechanism of transport is passive or active. The advantages of estuarine nursery areas for juvenile fishes have been often cited (McHugh 1967, Pearcy and Myers 1974, Boehlert and Mundy 1988). Estuaries commonly have greater food availability and protection from predation and adverse weather conditions.

As early development progresses, halibut may experience an increasingly higher range of temperatures due both to the distribution changes described above and to seasonal temperature differences. When eggs and young larvae are in nearshore waters of southern California during winter and spring, typical surface temperatures are about 13–17°C (Petersen et al. 1986). Juveniles in inshore waters during summer months commonly experience temperatures above 20°C, and shallow areas may be as warm as 24°C (Kramer 1990). Thus, one advantage of inshore migration might be higher temperatures, which could result in enhanced juvenile growth.

Fishes generally have temperature ranges at which growth and survival are optimum. These may differ with age; young of some species prefer warmer temperatures than adults (Norris 1963, McCauley and Huggins 1979). Early-life-history stages may also have different optimal temperatures, which may reflect field temporal and spatial distributions. For example, sole *Solea solea* larvae from North Sea coastal regions require

higher temperatures for successful development than sole eggs, probably because sole's spring spawning cycle results in larval abundances later in the season when sea temperatures are warmer (Irvin 1974, Fonds 1979).

Our purpose was to determine how growth and survival of California halibut may be influenced by temperature during development from egg to 3-month-old juvenile, and how optimal temperature ranges may change with ontogeny. Additionally, we were interested in how temperature may influence the timing of an important stage of flatfish development—settlement. We examined the possibility that month-old pelagic larvae passively transported to warmer inshore waters would settle significantly sooner due to a faster development rate than those remaining in colder offshore areas, resulting in selective settlement of shallow coastal nursery grounds. Larvae remaining pelagic due to colder waters would have a continued chance of transport inshore. The results of this study will aid in better understanding how oceanographic conditions may influence the survival of halibut early-life-history stages in the field.

Methods

Egg development

Eggs and sperm were stripped from ripe field-collected California halibut and combined in petri dishes. Approximately 300 fertilized eggs were placed in each of ten 3 L glass jars containing filtered, ultraviolet-light sterilized seawater (35‰) at an ambient temperature of 16°C. To establish and maintain desired temperatures, jars were placed in temperature-controlled water baths. A low level of aeration was provided in each jar to avoid the formation of temperature gradients. Soon after fertilization, temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C, resulting in two replicates of each temperature treatment. Light cycles simulated natural conditions (12L:12D). Every 2 hours until hatching, temperatures were recorded and at least five live eggs were sampled from each jar and preserved in 4% formalin. Because of the short experimental duration, water in the jars was not exchanged with fresh seawater during the experiment; when eggs in all jars had hatched or died, the experiment was terminated. To monitor development, egg series were examined using a dissecting microscope.

Larval growth and survival

An experiment was initially conducted to determine the influence of temperature on starvation rate of newly-hatched halibut larvae. Fertilized eggs were obtained from natural spawns from brood stock held in an outdoor 5 m diameter tank with a flow-through seawater system (for a further description of brood stocks, see Caddell et al. 1990). Seventy-five late-stage eggs (with developed embryos) were placed in each of ten 3 L glass jars of sterilized seawater at an ambient temperature of 16°C. Jars were in temperature controlled water baths and light aeration was provided. Temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C; each temperature treatment was replicated. Light cycles simulated natural conditions (12L:12D). Twenty percent of the water volume was replaced with fresh seawater twice weekly; at this time, ammonia and salinity levels were monitored. Dead halibut larvae were removed and counted daily until total starvation had occurred.

To determine how growth and survival of halibut larvae are temperature-dependent, the above experiment was repeated except food was added. Gadomski and Petersen (1988) found that for greatest survival, first-feeding halibut required food by the day of total yolk absorption. Full yolk depletion occurs 6 days after hatching at 16°C, but yolk absorption time varies with temperature (Gadomski et al. 1990). In the current study, we fed rotifers *Brachionus plicatilis* to halibut larvae after eye pigmentation and mouth development, but before total yolk absorption. Rotifers were stocked at 15/mL, following the methods of Gadomski et al. (1990), and supplemented thereafter as needed to maintain this density. Dead halibut larvae were removed and counted daily. Seventeen days after hatching, notochord lengths of surviving larvae were measured.

Because final survival was the same (zero) for all starvation trials, we compared survival curves of starved and fed larvae using the Mantel-Haenszel test (Matthews and Farewell 1985, Gadomski and Petersen 1988). This method tests the null hypothesis that incremental survival rates, computed between successive sampling times, are similar throughout the observation period. Rapid decomposition of deceased larvae resulted in accumulative totals of survivors and mortalities in some trials at the end of the experiment to be less than the original stocking density of 75. The Mantel-Haenszel test compensated for this by adding the "lost" mortalities to each experimental day proportionate to the known number that had died that day. First we tested if replicates could be combined; then we tested for a significant difference between survival curves of each experiment (starved and fed): 12°C vs. 16°C, 16°C vs. 20°C, and 20°C vs. 24°C. Because of

their similarity, survival curves of 12°C starved and 12°C fed trials were additionally compared.

For the fed trials, analysis of variance (ANOVA) was used to test for significant differences in final survival [ln(number alive+1)] and also differences in mean larval length between temperatures; if significant differences were found, Duncan's multiple range test was applied.

Juvenile growth and survival

Twenty-five 30-day-old pelagic larvae, which had been held at a mean ambient temperature of 16.7°C (SE 0.1), were stocked in each of twelve indoor 15 L black fiberglass tanks (40 cm diam., 12 cm depth) at 16°C. Water quality was maintained using a slow-drip flow-through system and tank aeration; ammonia and salinity levels were monitored weekly. A natural cycle of light and dark (12L:12D) was provided. Temperatures were raised using aquarium heaters in nine tanks 0.5°C per day from 16°C to 20, 24, and 28°C, resulting in three replicates per temperature. Fish were fed rotifers and newly-hatched brine shrimp nauplii (*Artemia* sp.) to excess. Dead fish were removed and counted daily and, in the last 15 days of the experiment, measured if not badly decomposed. The experiment was terminated when fish were 97 days old; survivors were counted and standard lengths determined. ANOVA and Duncan's multiple range test were utilized to test for significant differences in final survival and size between temperatures. Student's t-test was used to test for significant differences in mean standard lengths between 16°C and 20°C mortality and survivor groups.

Larval settlement

The settlement rate of a group of larvae held constantly at 16°C was compared with that of a group of larvae from the same cohort exposed to 20°C when a month old. These two temperature regimes were designed to simulate temperatures halibut larvae would encounter in the field if they (1) remained in colder offshore waters, or (2) were transported to warmer inshore areas when a month old.

Fifteen 30-day-old pelagic larvae that had been held at a mean temperature of 15.9°C (SE 0.1) were transferred to each of six indoor 15 L black fiberglass tanks at 16°C. Temperatures were raised 2°C a day to 20°C in three of the tanks while keeping three tanks at 16°C. Light cycles simulated natural conditions (12L:12D). Tanks were aerated to maintain water quality and avoid the formation of temperature gradients. Three times a week, 20% of the volume of water in each tank was replaced with fresh seawater; at this time, salinity and ammonia levels were monitored. Larvae were fed rotifers and newly-hatched brine shrimp to excess. Dead larvae were removed and counted daily. Each tank was observed for 10 minutes twice daily (morning and afternoon) and the numbers of settled and pelagic larvae counted; the mean values of these two daily observations were used to calculate percent settled larvae per tank per day. We defined "settled" larvae to be individuals that remained on the tank bottom (on their side) for at least 5 seconds during an observation period. This behavior occurs before metamorphosis is complete (Gadomski et al. 1990). When 100% settlement was observed in all tanks, fish were removed and standard lengths determined. Student's t-test was utilized to test for a significant difference in mean fish lengths between temperature treatments.

Results

Egg development

Halibut eggs are buoyant and about 0.8 mm in diameter with a single 0.14 mm oil globule. Eggs developed to hatching at 12, 16, and 20°C (Table 1). At 8°C, eggs did not develop beyond the 32-cell stage, and at 24°C cell divisions were abnormal and ceased during early development. Time to hatching was inversely propor-

Table 1

Egg development rates of California halibut *Paralichthys californicus* at five temperatures. Times (hours) after fertilization at which developmental events (I–VII) were first observed are presented. Two replicate jars were maintained at each temperature, with initially 300 recently-fertilized eggs per replicate; every 2 hours until hatching, at least five live eggs were sampled from each jar and egg development noted.

		Hours post-fertilization				
	Mean temp. (°C):	8.4	12.4	16.0	20.8	23.9
	SE (°C):	(0.2)	(0.1)	(0.1)	(0.1)	(0.6)
I	2–128 cells	4	4	2	2	2
II	Multicelled blastodermal cap	Dead	10	8	6	6
III	Germ ring >1/2 down yolk mass		26	18	14	Dead
IV	Embryo visible		32	22	16	
V	Blastopore closed		34	24	18	
VI	Tail separated from yolk mass		52	38	26	
VII	Eggs hatched		74	50	34	

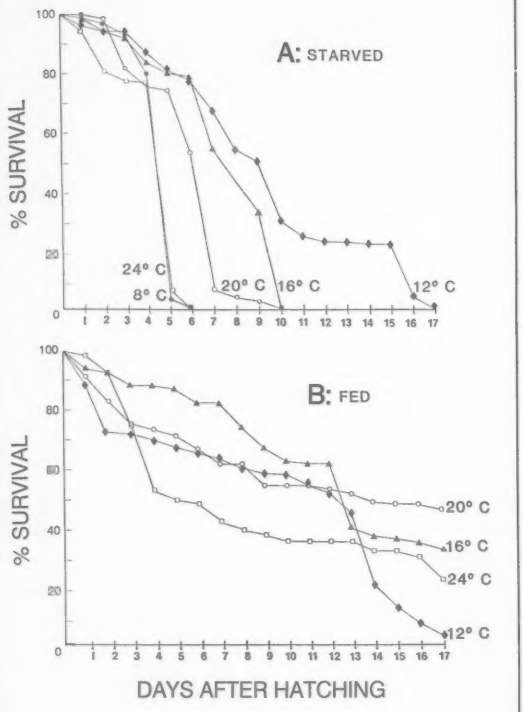

Figure 1

Survival (%) over a 17-day period of California halibut *Paralichthys californicus* larvae subjected to various temperatures. Groups of larvae were either (A) starved or (B) fed rotifers. Points are replicates (n 2) combined. Each replicate originally consisted of 75 individuals. The fed experiment did not include an 8°C trial because larvae at 8°C did not develop functional mouths or eyes and died with undepleted yolksacs.

Table 2

Mean notochord lengths of larval California halibut *Paralichthys californicus* 17 days after hatching at four temperature treatments. Two replicates were maintained at each temperature, with initially 75 late-stage eggs per replicate. N = combined number of surviving larvae in the two replicates.

Temperature (°C)			Notochord length (mm)	
Mean	SE	N	Mean	SE
12.3	(0.2)	4	3.92	(0.09)
16.2	(0.1)	45	4.80	(0.07)
20.0	(0.1)	69	5.31	(0.07)
24.1	(0.1)	34	5.94	(0.03)

tional to temperature: 74, 50, and 34 hours at 12, 16, and 20°C, respectively. Although not quantified, most eggs remaining (the initial number was reduced by sampling) at each temperature hatched. No abnormal yolksac larvae were observed.

Larval growth and survival

Replicates (n 2) of survival curves at each temperature for starved and fed larvae were combined for analysis since they were not significantly different ($P<0.05$). Survival curves of 12, 16, 20, and 24°C starved trials were significantly different ($P<0.01$), with starvation time (6–17 days) inversely proportional to temperature (Fig. 1A). Total mortality occurred first at temperature extremes, 8 and 24°C, which had similar mortality curves. Larval development at 8°C never progressed beyond the yolksac stage with unpigmented eyes and nonfunctional mouths (thus the fed experiment did not include an 8°C trial). At 24°C, however, dead larvae had pigmented eyes, functional mouths, and completely depleted yolks.

Survival curves of 20 and 24°C fed larvae were statistically similar, while the 12 and 16°C fed trials differed ($P<0.05$). At 24°C, mortality initially was high, perhaps due to temperature acclimation problems, but then mortality was gradual, paralleling the 20°C curve. At 16°C, survival initially was highest, but dropped after 12 days. Survival was high for fed larvae at 12°C until the end of the second week when the mortality rate increased, resulting in almost total mortality by day 17 (Fig. 1B). Although this survival pattern approximates the starved 12°C counterpart, the two curves are significantly different ($P<0.01$; more larvae in the fed trial survived longer). Fed larvae at 12°C initiated feeding (since food was observed in their guts) but survival enhancement was only short-term.

Final survival of fed larvae at 16°C was intermediate to final survival values at 20°C and 24°C; final survival was highest at 20°C and nearly zero at 12°C (Fig. 1B). Final survival did not significantly differ between temperature treatments (P 0.14), however. At experimental end, mean notochord lengths of surviving fed larvae were directly proportional to temperature (Table 2) and significantly different between all temperatures ($P<0.05$).

Juvenile growth and survival

Replicates (n 3) did not differ and were combined for analysis. Survival of 97-day-old fish at 16°C was significantly ($P<0.05$) lower than survival at 20, 24, or 28°C (Fig. 2); there were no significant survival differences between the three higher temperatures. Final mean standard length at 16°C did not differ signif-

Table 3

Mean standard lengths of 97-day-old juvenile California halibut *Paralichthys californicus* at four temperature treatments (acclimated when 1 month old from 16.7°C). Three replicates were maintained at each temperature, with initially 25 larvae per replicate. N = combined number of surviving juveniles in the three replicates.

Temperature (°C)			Standard length (mm)	
Mean	SE	N	Mean	SE
16.1	(0.1)	23	18.48	(0.93)
19.7	(0.0)	57	18.10	(0.39)
23.7	(0.1)	43	24.24	(0.57)
27.5	(0.0)	55	26.92	(0.71)

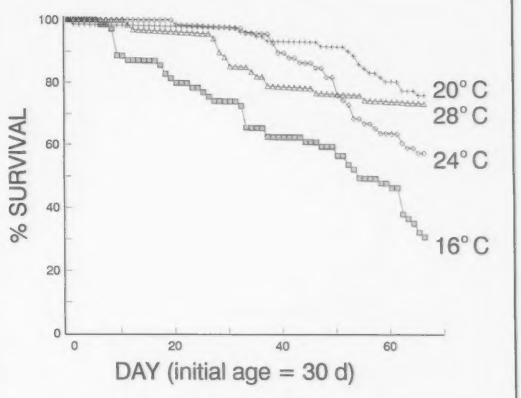

Figure 2

Survival (%) over a 67-day period of California halibut *Paralichthys californicus* larvae and juveniles at four temperatures. Larvae held at 16.7°C were transferred into experimental containers when 30 days old. Points are replicates (n 3) combined. Each replicate initially consisted of 25 larvae.

icantly from 20°C ($P<0.05$), but final mean length was significantly larger at 24°C, and larger at 28°C than 24°C (Table 3). These results were unexpected, since all previous experiments have demonstrated greater growth at 20°C than 16°C (Gadomski et al. 1990). Measurements of dead fish removed during the last 15 days of the experiment, however, indicated that smaller individuals were dying at 16°C than at 20°C, which biased the final growth data. Mean standard lengths at 16°C of fish that died during two time periods—the five (days 63–67) and fifteen (days 53–67) day intervals before the end of the experiment—were similar, 12.68 mm (SE 0.77, n 8) and 12.57 mm (SE 0.49, n 14), respectively, and were significantly smaller ($P<0.01$) than mean mortality lengths at 20°C for these same two time periods, 17.46 mm (SE 2.02, n 3) and 16.21 mm (SE 1.12, n 8). The mean standard length (12.68 mm, SE 0.77, n 8) of fish that died near the end of the experiment (days 63–67) at 16°C was also significantly smaller ($P<0.05$) than the final mean standard length of surviving individuals at 16°C, 18.48 mm (SE 0.93, n 23), indicating that size-selective mortality had occurred.

Larval settlement

There were no significant differences in survival between temperatures ($P<0.01$), with individual tank survival ranging from 80% to 93%. Larvae settled sooner at 20°C (actual mean temperature 20.0°C, SE 0.0) than 16°C (15.8°C, SE 0.1) (Fig. 3). At 20°C, 50% had settled by 6–8 days after transfer from 16°C, and all were settled by 10 days after transfer (when 40 days old). In contrast, at 16°C, 50% settlement did not occur until 12–15 days after transfer, and the last few larvae did not settle until 21–22 days (when 51–52 days old).

At the end of the experiment, larvae held at 20°C were significantly larger ($P<0.01$) than those at 16°C.

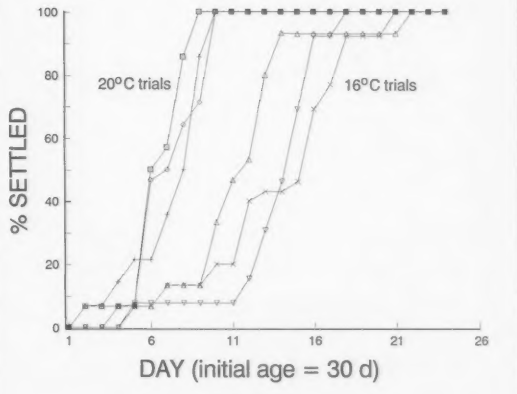

Figure 3

Percent of California halibut *Paralichthys californicus* settled per day at 16°C and 20°C. Larvae held at 16°C were transferred into experimental containers when 30 days old. Three replicate trials were conducted at each temperature. Each replicate initially consisted of 15 larvae.

At the beginning of the experiment (when transferred from 16°C), 30-day-old larvae had a mean length of 6.74 mm (SE 0.10, n 15) with 80% still exhibiting incomplete notochord flexion [the remaining 20% had achieved full flexion (standard length)]. All exhibited full elongation of the second to sixth dorsal rays

[dorsal ray elongation is characteristic of larvae of many pleuronectiform fishes; rays regress during metamorphosis (Ahlstrom et al. 1984, Gadomski et al. 1990)], and no eye migration was evident. At experimental end, 53-day-old larvae at 16°C had a mean length of 8.75 mm (SE 0.16, *n* 38), while at 20°C, mean larval length was 12.88 mm (SE 0.23, *n* 40). All fish at both temperatures had achieved standard length and had fully migrated eyes. Those at 16°C were somewhat less developed, however, since 8% still had slightly elongated dorsal rays. The remainder at 16°C and all fish at 20°C exhibited normal length dorsal rays characteristic of juveniles.

Discussion

Temperature tolerance experiments have been conducted on eggs and larvae of many fish species (Houde 1974, Laurence and Rogers 1976, Laurence 1978, Ferraro 1980, Bolla and Holmefjord 1988). The temperature tolerance range of California halibut eggs in the current study was at least 8 degrees (12–20°C), and probably more if the range endpoints fell between 8–12°C and 20–24°C. This 8-degree range is typical of other flatfish species such as English sole *Parophrys vetulus*, sole *Solea solea*, and winter flounder *Pseudopleuronectes americanus* (Alderdice and Forrester 1968, Irvin 1974, Fonds 1979, Buckley 1982). Absolute temperatures tolerated varied among species, however, and were reflective of field habitat temperatures; sole *S. solea* eggs survived slightly lower temperature exposures than halibut (8–16°C), whereas English sole and winter flounder eggs (found in colder waters) tolerated much lower temperatures, 4–12°C and 2–10°C, respectively.

Temperature tolerance ranges may change with ontogeny. Halibut larvae exhibited a higher temperature tolerance range (16–24°C) than halibut eggs, a pattern which has also been demonstrated for sole *S. solea* (Irvin 1974, Fonds 1979) and yellow perch *Perca flavescens* (Hokanson and Kleiner 1974). Additionally, sole (Devauchelle et al. 1987) and yellow perch (Hokanson and Kleiner 1974) temperature tolerances were higher for late-stage eggs than for eggs at early developmental stages. Similarly in our study, larval halibut experiments initiated with late-stage eggs resulted in a higher range of temperature tolerance than experiments initiated with recently fertilized eggs. As larval halibut development progressed, temperature tolerance ranges also increased; soon after hatching, the highest mortality rate occurred at 24°C, whereas mortality of older larvae was greater at 12°C and 16°C (Fig. 1B).

At low temperatures, biochemical reactions, and thus metabolic rates and growth, of poikilotherms are reduced (Laurence 1975). For all halibut early-life-history stages, the lowest tested temperatures adversely affected growth and survival. Larval halibut may have a minimum necessary growth rate for survival, as suggested by Gadomski and Petersen (1988), and reported for larvae of other fish species (Jones 1973, Beyer and Laurence 1980, Govoni et al. 1986). At 8°C, development of halibut larvae halted soon after hatching when larvae still had significant amounts of yolk, unpigmented eyes, and nonfunctional mouths. Ehrlich and Muszynski (1982) found that at low temperatures, yolk-sac California grunion *Leuresthes tenuis* encountered problems with fat metabolism. At 12°C, survival of fed halibut larvae initially was high and ingestion was observed, but by 17 days after hatching almost all larvae were dead. This type of survival pattern was also reported by Laurence (1975) for winter flounder *Pseudopleuronectes americanus*, which survived in the laboratory at 2°C for 5 weeks with a very slow development rate, and then died before metamorphosis; larvae at higher temperatures of 5 and 8°C developed normally. Similarly, Laurence (1978) found that larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* could only survive for limited periods after hatching at lower tested temperatures, with variable and elevated oxygen consumptions indicating physiological stress.

The temperature tolerance ranges of halibut eggs and larvae in the laboratory approximate temperatures these stages usually encounter in the field; deviations from normal sea temperatures could affect survival. During winter and spring, nearshore (1–20 km from shore) sea surface temperatures off southern California usually range between 13 and 17°C (Petersen et al. 1986). Vertical mixing during the winter season generally produces uniform temperatures throughout the water column. In late-spring and summer, surface waters warm as high as 20–22°C, and a thermocline develops (Petersen et al. 1986). Late-spring and summer upwelling events may disrupt this temperature stratification, however, transporting deep colder waters to the surface (Dorman and Palmer 1981). Our study has shown that halibut larvae can endure 12°C for a short period during the first 3 weeks after hatching, but years with prolonged periods of this temperature might result in high larval mortality. Since 1920, there have been only three instances when surface temperatures at the Scripps Pier off San Diego remained below 12.5°C for as long as 2 weeks, and these were all in the time period of December–February (E. Stewart, Scripps Inst. Oceanogr., La Jolla, CA). Temperatures considered lethal for halibut eggs and larvae (≤8°C) were never recorded at this site. In

contrast, areas north of Point Conception, California commonly have extended periods of temperatures below 12°C (SIO 1955–85, Parrish et al. 1981). Low northern California ocean temperatures may possibly limit the geographic range of larval halibut abundance, although areas off northern California are also characterized by strong offshore surface transport (due to upwelling), which in itself limits survival of pelagic fish eggs and larvae (Parrish et al. 1981).

Growth and development rates of halibut eggs and larvae in the laboratory increased with temperature increase. We did not determine the upper temperature tolerance limit of halibut larvae, but the highest temperature tested, 24°C, exceeds normal southern California ocean temperatures. Swift development of pelagic eggs and larvae in the field may be advantageous, since these stages are particularly vulnerable to predation (Bailey 1981). Conversely, faster development requires that more food be available, or starvation may quickly occur; we found that newly-hatched halibut larvae died sooner from starvation at higher temperatures (Fig. 1A), since yolk absorption was faster. Thus, warm ocean temperatures would increase starvation-related mortality of larval halibut in the field during periods with inadequate available food, while cold temperatures might decrease mortality.

Juvenile halibut had a higher temperature tolerance range than halibut eggs and larvae; survival of 3-month-old halibut was significantly lower at 16°C than at 20–28°C. Juvenile growth rates at 20, 24, and 28°C were directly proportional to temperature. Surviving juveniles were similarly sized at 16°C and 20°C (Table 3), but this final size data are biased because fish that died at 16°C were significantly smaller than those that died at 20°C. The less robust, slower-growing fish at 16°C died, perhaps indicating that young juveniles, like larvae (Laurence 1977, Houde and Schekter 1980), require a minimum growth rate for survival that was unattainable for some individuals at 16°C.

The higher temperature range required for best survival of juvenile halibut reflects observed spatial and temporal distribution patterns. High densities of newly-settled larval and juvenile halibut have been collected during spring and summer in southern California bays where waters may be as warm as 24°C (Allen 1988, Kramer 1990); solar heating of very shallow waters could result in even higher temperatures. Juveniles in shallow areas of bays and estuaries may thus have the advantage of enhanced growth and survival due to warmer waters, in addition to other advantages, such as increased food availability and protection. Larval cohorts that settle and remain in open-coast areas do not have these advantages, and could experience low survival. As an example of this, in 1988 Kramer (1990, 1991) collected most newly-settled halibut juveniles in open-coast areas, whereas bays contained larger sized juveniles; Kramer suggested that individuals that settled on the open coast eventually moved into bays or died. However, Kramer (1991) did not find a significant difference in growth rates of smaller juveniles ($\leq$40 mm standard length) from bay versus coastal locations.

The El Niño years of 1982 and 1983 may be an example of warm ocean temperatures enhancing juvenile halibut survival, both in open-coast areas and during normally colder seasons. Higher densities of juvenile halibut were collected in bays in 1983 (Allen 1988). Additionally, strong fishery catches of halibut 1982 and 1983 year-classes have been reported (Miller 1990, Pattison and McAllister 1990).

The mechanism of larval or juvenile halibut entry into bays, and the stage at which entry occurs, are unknown. Kramer (1990) found newly-settled halibut almost exclusively in southern California bays in 1987, whereas in 1988 most settled in shallow open coast areas and then possibly moved into bays. English sole *Parophrys vetulus* have been reported to enter bays both during and after metamorphosis (Misitano 1976, Boehlert and Mundy 1987, Rogers et al. 1988). Plaice *Pleuronectes platessa* settle in deeper waters and move into shallow areas after metamorphosis (Lockwood 1974). For both English sole and plaice, tidal stream transport is an important migration mechanism (van der Veer and Bergman 1986, Boehlert and Mundy 1987). Other physical factors that have been suggested to mediate shoreward migration of larval and juvenile fishes are often associated with river discharge (salinity; olfactory cues) (Creutzberg 1961, Boehlert and Mundy 1987), and are thus not as applicable in drier southern California, where rainfall is only 25–40 cm/year (Petersen et al. 1986). Temperature differences between near and offshore areas might be an important cue (Boehlert and Mundy 1988, Miller 1988), although the ability of halibut larvae and young juveniles to seek preferred temperatures has not been demonstrated.

High inshore densities of juvenile halibut are likely a combination of passive larval transport to coastal areas, followed by active inshore movement of larvae or juveniles mediated by environmental stimuli. Shoreward transport of pelagic fish eggs and larvae to coastal nursery grounds has been demonstrated to enhance cohort survival (Nelson et al. 1976, Parrish et al. 1981). Onshore and offshore surface water transport in nearshore southern California areas is sporadic and associated with late-spring and summer downwelling and upwelling events (Winant 1980, Dorman and Palmer 1981). Another possible mechanism of onshore transport is surface slicks generated by tidally forced internal waves (Kingsford and Choat 1986, Shanks

1988). Additionally, halibut eggs and larvae may be transported parallel to the shore, since a narrow nearshore current with a generally southward surface flow often occurs within 10–20 km of the coast (Tsuchiya 1980, Winant and Bratkovich 1981).

The passive transport of pelagic halibut larvae off southern California is thus influenced by a variety of currents and oceanographic conditions. Our results indicate that halibut larvae that encounter warmer waters during transport may settle much sooner than those remaining in colder waters (Fig. 3). Therefore, larvae carried by alongshore currents might eventually settle near the entrances of bays or estuaries due to warmer waters in these areas. Larvae transported offshore during upwelling events would experience lower temperatures (Dorman and Palmer 1981), resulting in delayed settlement and the possibility of eventual shoreward transport into shallow coastal or inshore nursery areas where warm temperatures could stimulate settlement.

The ability of pelagic larvae of many marine invertebrates to delay settlement until an appropriate habitat is available has been well documented (Scheltema 1974, Doyle 1975). Fish larvae have not commonly been demonstrated to have this ability, although Victor (1986) reported that bluehead wrasse *Thalassoma bifasciatum* can extend the duration of the planktonic larval period after attaining settlement size by reducing growth rate. We found that halibut larvae at 16°C took about a week longer to 50% settlement than larvae reared initially at 16°C and then exposed to 20°C when 1 month old; one individual at 16°C was pelagic 12 days after all larvae had settled at 20°C (Fig. 3). Although the observed longer period to settlement at 16°C vs. 20°C was to some degree a direct growth response to temperature, halibut larvae in colder waters may additionally be capable of delaying settlement for a limited period until encountering the appropriate cue, higher temperatures. This trait would enhance larval halibut survival by increasing the likelihood of settlement in warmer inshore areas.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Growth Parameters from Tagging Data, using von Bertalanffy Models Incorporating Individual Variation

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Abstract. – Von Bertalanffy growth models appropriate for fitting to length-increment data by maximum likelihood are described. Models incorporating variation in growth among individuals, release-length-measurement error, and model error are developed and fit to southern bluefin tuna *Thunnus maccoyii* tag-return data. On the basis of likelihood ratio tests, a model in which individual variation in growth is represented by variation in L_∞ and which explicitly incorporates model error is selected as the most appropriate model for these data. The parameter estimates obtained were μ_{L_∞} = 186.9 cm, $\sigma_{L_\infty}^2$ = 218.8 cm², K = 0.1401/year, and σ_ϵ^2 = 15.25 cm². Analyses of simulated data suggest that biased estimates of growth parameters can result if model error is not explicitly included in von Bertalanffy models incorporating individual variation in growth.

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Knowledge of the growth of a fish and, in particular, a mathematical description of the increase in length or weight with time, is important for understanding its population and fishery dynamics. Also, fish growth has been used directly or indirectly to calculate catch age composition (Hayashi 1974, Baglin 1977, Kume 1978, Skillman and Shingu 1980, Majkowski and Hampton 1983), mortalities (Beverton and Holt 1957, Pauly 1987) and yield-per-recruit (Beverton and Holt 1957, Ricker 1975) and to make inter- and intra-population comparisons (Brousseau 1979, Goldspink 1979, Kohlhorst et al.1980, Francis 1981).

Techniques for studying fish growth in length fall into three categories: (i) Direct measurements of age (such as those obtained by counting periodic protein and calcium depositions in scales, otoliths, vertebrae, fin rays, or some other hard tissue) and length; (ii) analysis of time series of length-frequency data (sometimes called modal progression analysis); and (iii) analysis of length-increment and time-at-liberty data from a mark-recapture experiment. In each case, a growth model is usually fit to the data. Various models have been proposed for fitting to these types of data (e.g., Brody 1927 and 1945, Ford 1933, Walford 1946, Richards 1959, Knight 1969), but by far the most used model in fisheries research is that of von Bertalanffy (1938). This model, originally formulated on physiological considerations, has three parameters that have the biological interpretations of average maximum length (L_∞), the average rate at which L_∞ is approached (K), and the theoretical average time at which length would be zero if growth had always occurred according to the model (t_0).

The study of growth by direct measurements of age (reviewed by Bagenal 1974, Brothers 1979, Beamish 1981, Prince and Pulos 1983) and length is not possible for many species. In particular, good estimates of the ages of older fish are frequently hard to come by. This was the case for Yukinawa's (1970) study of southern bluefin tuna *Thunnus maccoyii* age and growth from presumed annual rings on scales. He examined the scales of 2240 fish within the length range of 38–184 cm, but was able to age only about 15% of fish larger than 120 cm, and none of those larger than 153 cm. Similarly, Thorogood (1986) was unable to age significant numbers of large southern bluefin from examinations of their otoliths.

A major aspect of length-frequency analysis is the identification of age classes in the data. To do this, Harding (1949) and Cassie (1954) used probability paper, and Tanaka (1956) fit parabolas to the logarithms of

observed length-frequencies. More recently, digital computers have been used, and the distribution of length-at-age has been assumed to be normal or log-normal (Hasselblad 1966, Kumar and Adams 1977, Macdonald 1969 and 1975, Macdonald and Pitcher 1979, Schnute and Fournier 1980, Fournier and Breen 1983). Pauly's method (Pauly 1987) of fitting growth curves to observed peaks in a time series of length-frequency data, commonly known as ELEFAN I, has received some recent attention, but it suffers from the assumption that length-at-age does not vary (Hampton and Majkowski 1987).

Some attempts have been made to study the growth of southern bluefin, using length-frequency data. Serventy (1956) plotted the progressions of length-frequency means and modes of juvenile age classes caught in Australian coastal waters, but did not attempt to quantify the results as a growth equation. Robins (1963) made the first attempt to quantify growth, obtaining a Walford growth transformation from an analysis of length-frequency modes of juvenile fish. Hearn (1986) identified a seasonal component to growth from analyses of similar data. Recently, promising results have been obtained with the application of MULTIFAN, a likelihood-based method for estimating von Bertalanffy growth parameters from length-frequency data, to southern bluefin tuna data (Fournier et al. 1990).

Length-increment and time-at-liberty data from a tagging experiment provide direct measurements of the growth of individual fish as long as the tag or the tagging procedure does not have a significant effect on growth. Using a von Bertalanffy model and a fitting procedure such as that proposed by Fabens (1965), estimates of L_∞ and K can be obtained, but without additional assumptions no estimate of t_0 is available.

Murphy (1977) analyzed the release and recapture data from 2578 tagged southern bluefin and derived estimates of L_∞ and K that he considered to be more reliable than those previously derived by other workers. Kirkwood (1983) obtained similar estimates from a smaller data set (n 794), excluding fish that had been at liberty for less than 250 days. In addition, he incorporated age-at-length observations from length-frequency modes to the estimation procedure to obtain an estimate of t_0.

None of the studies of southern bluefin growth, and indeed few studies of fish growth in general, take explicit account of variation in growth among individuals by the incorporation of parameters describing such variation into the model. Krause et al. (1967) gave the first thorough treatment of individual variability in growth when deriving conditional probability densities for body weight-at-age of chickens. Sainsbury (1980) recognised the importance of individual variability in fishes showing von Bertalanffy growth, and derived equations appropriate for length-at-age and length-increment data if both L_∞ and K showed individual variation. He also showed that biased estimates of mean growth parameters could result if individual variability in K existed and was ignored. Kirkwood and Somers (1984) developed a simpler model for length-increment data in which only L_∞ was variable and applied it to two species of tiger prawn.

A problem with these models (as pointed out by Kirkwood and Somers 1984) is that all the observed "error" is attributed to individual variation in L_∞ and/or K. It is, of course, reasonable to expect that there will also be error due to some animals not growing exactly according to the von Bertalanffy model, a so-called model error. For standard growth models not incorporating individual variability, all residual error is assumed to be model error. It is also reasonable to expect that, in the case of length-increment data, the initial or release length cannot always be measured exactly and therefore will be an additional source of error.

In this paper, southern bluefin tuna tag-return data are analysed using three existing models, all of which are based on the von Bertalanffy model: the standard model, using the fitting procedure described by Fabens (1965), model (2) of Kirkwood and Somers (1984), and the Sainsbury (1980) model. In addition, models based on the latter two that incorporate model error and release-length-measurement error are derived and applied. The properties and assumptions of each of the models are investigated using computer simulation techniques.

Methods

Tagging methods and data

The primary method used to catch fish for tagging was commercial pole-and-line, using either live or dead bait, although on some occasions trolling was also used. Prior to release, the fork lengths of most fish selected for tagging were measured to the nearest centimeter on a measuring board. While the fish were restrained on the measuring board, one or two numbered tuna tags, each consisting of a molded plastic barbed head with a tubular plastic streamer glued to it (Williams 1982), were inserted forward into the musculature at an angle of about 45°, 1–2 cm below the posterior insertion of the second dorsal fin. For double-tagged fish, one tag was inserted on each side of the second dorsal fin. Ideally, the tag barb was anchored behind the second dorsal fin ray supports (pterygiophores).

The primary data used in this study consist of returns of southern bluefin tagged between 1962 and 1978 that were measured to the nearest centimeter at release, were thought to have reliable dates of release and

recapture, and were at liberty for at least 250 days. These criteria were satisfied by 1800 returns. The last criterion was applied to eliminate the possible effect that the tagging operation might have on length growth and to minimize the biasing effect that seasonal fluctuations in growth, if present, might have on parameter estimation.

Most fish were 50–80 cm long when tagged, with the smallest 38 cm and the largest 104 cm. The range of recapture lengths was 51–185 cm, with most being in the range 60–100 cm. The times at liberty for the primary data set range from 250 days (the minimum allowed) to approximately 11 years.

Parameter estimation

Model 1: Standard von Bertalanffy model The form of the von Bertalanffy growth model appropriate for fitting to tag-return data (indexed by i) is, as described by Fabens (1965),

$$\delta l_i = (L_\infty - l_i)(1 - e^{-Kt_i}) + e_i \qquad (1)$$

where δl_i is the length increment, l_i is the release length, t_i is the time at liberty, and e_i is a model error term (or residual), all for the i th observation. The error term e_i is assumed to be a normally-distributed random variable with an expected value of zero and variance σ_e^2. Thus, for given l_i and t_i, δl_i is a normally-distributed random variable with an expected value of $(L_\infty - l_i)(1 - e^{-Kt_i})$ and a variance of σ_e^2. Estimates of L_∞, K, and σ_e^2 can be obtained by nonlinear ordinary least squares (as in Kirkwood and Somers 1984) or by maximum likelihood (Kimura 1980). In the case of model 1, either technique can be applied, since the variance of δl_i is assumed to be constant with increasing t_i. However, in the models that incorporate individual variability (see below), the variance of δl_i increases with increasing t_i. This would require the use of weighted least-squares if this approach was followed. Since the weights would depend on the estimated K, an iterative procedure would be necessary to obtain the appropriate estimates. Therefore, the maximum-likelihood method, which is far more straightforward, is used to obtain parameter estimates for this and the models that follow.

For n observations of δl_i and t_i ($i = 1$ to n), the likelihood function is

$$L = \prod_{i=1}^{n} (2\pi\sigma_e^2)^{-\frac{1}{2}} \exp\left[-\frac{[\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2} \right],$$

and estimates of L_∞, K, and σ_e^2 are found by minimizing

$$LL = -\ln L = \frac{n}{2} \ln (2\pi\sigma_e^2) + \frac{\sum_{i=1}^{n} [\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2}.$$

This was accomplished for all the models described in this paper, using the minimization subroutine MINIM (programmed by D.E. Shaw, CSIRO Div. Math. Stat., P.O. Box 218, Lindfield 2070, Aust.), which uses the method of Nelder and Mead (1965). Equivalent subroutines are available in several commercially-available software packages.

Model 2: Kirkwood and Somers model Kirkwood and Somers (1984) described a model which allowed for individual variation in growth through an individually variable L_∞. Specifically, L_∞ was assumed to be normally distributed with mean μ_{L_∞} and variance $\sigma_{L_\infty}^2$. For given l_i and t_i, δl_i is a normally-distributed random variable whose expected value is given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-Kt_i}) \qquad (2)$$

and variance by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2.$$

The negative log-likelihood function now becomes

$$LL = \sum_{i=1}^{n} \frac{\ln [2\pi \text{ var}(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2 \text{ var}(\delta l_i)} \qquad (3)$$

from which maximum likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, and K may be obtained.

Model 3: Kirkwood and Somers model with model error Let us now assume that the variance of δl_i is comprised of components due to both the individual variation in L_∞ and to a normally-distributed model error, e_i, having a mean of zero and variance σ_e^2. In this case, $E(\delta l_i)$ is unchanged from Equation (2) and the variance of δl_i is given by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2 + \sigma_e^2. \qquad (4)$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, and σ_e^2 can again be obtained by substituting the right sides of Equations (2) and (4) into Equation (3).

Model 4: Kirkwood and Somers model with model error and release-length-measurement error Because the tagging operation involves the handling of powerful, often violently struggling fish, it is quite reasonable to expect that release length will be measured with error. If possible, this error should be independently estimated and included in the growth model. On the other hand, measurement of a dead fish at recapture should not involve a significant error if competently carried out. In this study, recapture lengths are assumed to be measured without error.

If growth is assumed to be negligible, a comparison of lengths-at-release and lengths-at-recapture (l_2) for animals at liberty for a very short time should provide a good estimate of release-length-measurement error. Such a comparison was made for 251 tag returns in which the release length was 50 cm or more (see Residuals Analysis section) and the period at liberty was 10 days or less. For this data set, the mean measurement error $\mu_m = (\Sigma\{l_2 - l_1\}/251)$ was 0.4861 cm with a variance, σ_m^2, of 5.2428 cm^2. At least some of this μ_m might be attributed to growth, since the average growth increment over a 10-day period is approximately 0.5 cm. In this paper, μ_m is assumed to be zero.

Because δl_i now depends on another random variable (l_i), it is convenient to assume that the length-at-recapture is a normally-distributed random variable. Equation (1) can be modified to describe the i th recapture length as

$$l_{2i} = [\mu_{L_\infty} - (l_i + \varepsilon_i)]\,[1 - e^{-Kt_i}] + l_i + \varepsilon_i + e_i, \qquad (5)$$

where ε_i is the normally-distributed release-length-measurement error. The expected value of l_{2i} is given by

$$E(l_{2i}) = [\mu_{L_\infty} - E(l_i)]\,[1 - e^{-Kt_i}] + E(l_i),$$

where $E(l_i)$ is equal to $l_i + \mu_m$. Collecting terms in ε_i, Equation (5) is rewritten as

$$l_{2i} = [\mu_{L_\infty} - l_i]\,[1 - e^{-Kt_i}] + l_i + e^{-Kt_i}\,\varepsilon_i + e_i.$$

The variance of l_{2i} is then given by

$$\text{var}\,(l_{2i}) = \sigma_{L_\infty}^2\,(1 - e^{-Kt_i})^2 + \sigma_e^2 + \sigma_m^2\,e^{-2Kt_i}.$$

Given estimates of μ_m and σ_m^2, maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, and σ_e^2 can be obtained as before.

Model 5: Sainsbury model Sainsbury (1977, 1980) described a model that recognised individual variation in K, as well as in L_∞. He assumed that both were independent random variables, with K following a gamma distribution and L_∞ being normally distributed. He also assumed that, as an approximation, δl_i is normally distributed for given l_i and t_i, pointing out that this should involve little error if L_∞ is normally distributed (Sainsbury 1977). With μ_K and σ_K^2 denoting the mean and variance, respectively, of K, the relevant equations are

$$E(\delta l_i) = [\mu_{L_\infty} - l_i]\left[1 - \left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}\right]$$

and

$$\text{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}^2 + C_2\,(\mu_{L_\infty} - l_i)^2, \qquad (6)$$

where

$$C_1 = 1 - 2\left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}} + \left[1 + \frac{2\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}$$

and

$$C_2 = \left[1 + \frac{2\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}} - \left[1 + \frac{\sigma_K^2\,t_i}{\mu_K}\right]^{-\frac{2\mu_K^2}{\sigma_K^2}}$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, μ_K, and σ_K^2 can be obtained as shown earlier.

Model 6: Sainsbury model with model error As shown in model 3, a model error can be included simply by adding the model error variance term to Equation (6) giving

$$\text{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}^2 + C_2\,(\mu_{L_\infty} - l_i)^2 + \sigma_e^2.$$

Solution by maximum likelihood now requires that a fifth parameter, σ_e^2, be estimated from the data.

Model 7: Sainsbury model with model error and release-length-measurement error Using logic similar to that developed in model 4, length-at-recapture is now considered as the random variable and assumed

to be normally distributed, with

$$E(l_{2i}) = [\mu_{L_\infty} - E(l_i)]\left[1 - \left[1 + \frac{\sigma_K^2 t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}\right] + E(l_i) \quad (7)$$

and

$$\text{var}(l_{2i}) = C_1 \sigma_{L_\infty}{}^2 + C_2 [\mu_{L_\infty} - E(l_i)]^2 + \sigma_e^2 + \sigma_m^2 E(e^{-2Kt_i}), \quad (8)$$

where

$$E(e^{-2Kt_i}) = \left[1 + \frac{2\sigma_K^2 t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}$$

Given the estimate of σ_m^2 derived for model 4, maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}{}^2$, μ_K, σ_K^2, and σ_e^2 can be obtained as before.

Estimation of t_0 An estimate of t_0 is required for many applications of the von Bertalanffy model, but this parameter cannot be estimated from tag-return data alone. To estimate t_0, one or more observations of age-at-length are required. Kirkwood (1983) described a maximum-likelihood method for determining t_0, along with L_∞ and K, if supplementary age-length data are available in addition to tag-return data. Such data can easily be accommodated in the models described above. Consider the case where n1 tag returns (δl_i and δt_i) and n2 age-length observations (l_j and t_j) are available. We now have two random variables, δl_i and l_j, which have normal probability density functions conditioned on l_i (release length) and δt_i, and t_j, respectively. Their expected values, for example in the case of model 3, are given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-K\delta t_i})$$

$$E(l_j) = \mu_{L_\infty}(1 - e^{-K(t_j - t_0)})$$

and their variances by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}{}^2 (1 - e^{-K\delta t_i})^2 + \sigma_{e1}^2$$

$$\text{var}(l_j) = \sigma_{L_\infty}{}^2 (1 - e^{-K(t_j - t_0)})^2 + \sigma_{e2}^2$$

where σ_{e1}^2 and σ_{e2}^2 are independent model error variances. Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}{}^2$, K, t_0, σ_{e1}^2, and σ_{e2}^2 could, in theory, be found by minimizing

$$LL = \sum_{i=1}^{n1} \frac{\ln[2\pi \text{ var}(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2 \text{ var}(\delta l_i)} + \sum_{j=1}^{n2} \frac{\ln[2\pi \text{ var}(l_j)]}{2} + \frac{[l_j - E(l_j)]^2}{2 \text{ var}(l_j)}. \quad (9)$$

However, the estimation of six parameters (or seven in the case of models 6 and 7) may prove unrealistic in many cases. In order to obtain an approximate estimate of t_0, I have employed a simpler procedure. It involves fixing the growth parameters estimated from tag-return data and estimating t_0 by minimizing only the second summation in Equation (9), using the same approximate age-length data as Kirkwood (1983). I did not attempt to estimate simultaneously all parameters using the combined length-increment and age-length data because of the approximate nature of the latter data.

Model selection

An important part of this study was to select the most appropriate growth model for use in southern bluefin tuna stock assessments. Although L provides a means of comparing the goodness of fit of the various growth models with the tagging data, it is not immediately clear whether the more complex models result in a statistically-significant improvement in fit to the data. Likelihood ratio tests (Mendenhall and Scheaffer 1973, Kendall and Stuart 1979, Kimura 1980) can be used to address this question.

Likelihood ratio tests Let λ be defined by

$$\lambda = \frac{L(\phi_0)}{L(\phi_a)},$$

where $L(\phi_0)$ and $L(\phi_a)$ are the maximum-likelihood function values under the null hypothesis (the simple model is correct) and the alternative hypothesis (the more complex model is correct), ϕ_0 is the set of maximum-likelihood estimates of r parameters under the null hypothesis, and ϕ_a is the set of maximum-likelihood estimates of r + s parameters under the alternative hypothesis. Under certain regularity assump-

tions that hold under most circumstances for large sample sizes (Mendenhall and Scheaffer 1973), $-2\log_e\lambda$ behaves as a χ^2 random variable with s degrees of freedom. Therefore $-2\log_e\lambda$ may be compared with a critical χ^2 value (pertaining to a suitable rejection region) and the null hypothesis either accepted or rejected. For example, a value of $-2\log_e\lambda$ of more than 3.84 would lead to rejection of the simple model in favor of a model with one extra parameter (df 1) with a rejection region (significance level) of 0.05 on the χ^2 distribution.

Simulations

Assessment of model performance One hundred simulated data sets were produced and analysed by the models described above. The simulated data sets were produced by simulating values of δl_i (for each of the 1736 observations comprising the edited data set), using the following equation,

$$\delta l_i = [L_{\infty i} - (l_i + \varepsilon_i)]\,[1 - e^{-K_i t_i}] + e_i.$$

$L_{\infty i}$ and e_i were sampled from normal distributions, and K_i from a gamma distribution defined by the model 7 maximum-likelihood estimates of their respective μ's and σ^2's. The release-length-measurement error, ε_i, was sampled from a normal distribution with a mean of 0 and a variance of 5.2428 cm^2. Subroutine GGNML of the International Mathematical and Statistical Library (IMSL) was used to generate random normal deviates. IMSL subroutine GGAMR was used to generate gamma deviates. Actual values of l_i and t_i from the edited data set were used.

A second set of simulations was undertaken, assuming $L_{\infty i}$ and K_i to be correlated with a correlation coefficient of 0.80. Correlated normal deviates were generated, using IMSL subroutine GGNSM. This was done to test the sensitivity of the models to the assumption of independence of $L_{\infty i}$ and K_i observations. In this set of simulations, K was assumed, for simplicity, to be normally distributed, rather than gamma distributed. With the values of μ_K and σ_K^2 encountered in this study, the gamma and normal distributions are virtually indistinguishable, and therefore the normal approximation should result in little or no error. This was confirmed in a small number of simulations where analyses of simulated data, produced using normally-distributed K_i values (uncorrelated with $L_{\infty i}$), gave results virtually identical to simulations where K_i was gamma distributed.

Analysis of the 100 simulated data sets by each of the models described above provided 100 sets of parameter estimates for each. The means and standard errors of these estimates were calculated to (i) derive approximate confidence intervals for the maximum-likelihood estimates produced by the models and (ii) compare model performance, i.e., their ability to estimate known parameter values.

Testing the assumption of normally-distributed l_{2i} The assumption that, given l_i and t_i, the random variable δl_i (or l_{2i} in the case of models 4 and 7) is normally distributed, is central to all the models described. This assumption is most questionable for model 7, where K variability and release-length-measurement error could have unpredictable effects on the distribution of l_{2i}. This assumption was tested for 30 combinations of l and t by generating 5000 values of l_{2i} for each combination, using the following equation.

$$l_{2i} = [L_{\infty i} - (l + \varepsilon_i)]\,[1 - e^{-K_i t}] + l + \varepsilon_i + e_i.$$

A χ^2 goodness-of-fit test (IMSL subroutine GPNOR) with 50 equiprobable categories was then applied to identify possible departures from a normal distribution with mean and variance given by Equations (7) and (8), respectively. Values of l of 50, 60, 70, 80, 90, and 100 cm were combined with values of t of 2, 4, 6, 8, and 10 years to produce the 30 combinations.

Results

Residuals analysis

Using model 1, an analysis of residuals was carried out on the primary data set. An initial fit of model 1 to the 1800 observations yielded estimates of L_∞, K, and σ_e^2 of 195.614 cm, 0.131914/year, and 24.8193 cm^2, respectively. Standardized residuals ($R_i = e_i/\sigma_e$) were calculated and plotted against t_i (Fig. 1) and against l_i (Fig. 2). Examination of Figure 1 reveals an even distribution of standardized residuals about zero and no obvious relationship with time at liberty. However, Figure 2 suggests that the fit model may not be appropriate over the entire range of release lengths observed. For release lengths less than 50 cm, there are 54 positive residuals but only 8 negative residuals, indicating that observed growth was faster than the model would predict for these smaller fish. For release lengths of 50 cm and larger, the pattern of residuals is unremarkable. On this basis, observations with release lengths smaller than 50 cm were excluded from further analyses.

A refit of model 1 to the amended data set (1738 observations) provided estimates of L_∞, K, and σ_e^2 of 200.120 cm, 0.125836/year, and 23.6157 cm^2, respectively. Using these parameter estimates, standardized

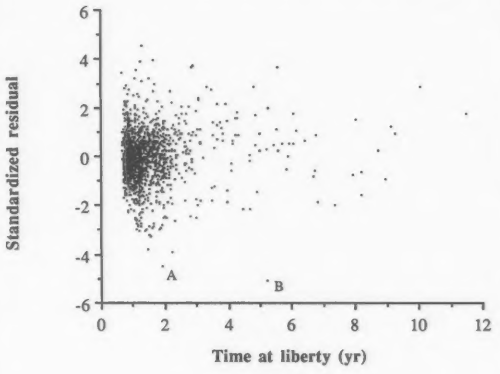

Figure 1

Plot of standardized residuals against time-at-liberty following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were $L_\infty = 195.614$ cm, K = 0.131914/year, and $\sigma_e^2 = 24.8193\,cm^2$. The observations labeled A and B are those identified as outliers.

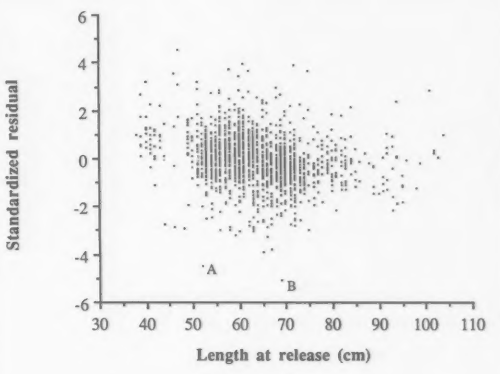

Figure 2

Plot of standardized residuals against release length following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were $L_\infty = 195.614$ cm, K = 0.131914/year, and $\sigma_e^2 = 24.8193\,cm^2$. The observations labeled A and B are those identified as outliers.

residuals were recalculated and checked for outliers. Models 2–7 incorporate individual variability in growth parameters, necessitating the use of a quite severe criterion in the definition of an outlier. An observation was classified as an outlier only if the absolute value of its standardized residual was greater than 4.4172. Under the assumptions of model 1, only one in 2000 observations would exceed this value due to chance alone. Two observations were classified as outliers on this basis and rejected from further analyses. These observations are indicated in Figures 1 and 2. The final data set to which all models were fitted consisted of 1,736 observations.

Parameter estimates

Parameter estimates for the seven models fitted to the final data set are given in Table 1. The estimates differ substantially among some models, which is not surprising since they are based on rather different assump-

Table 1

Southern bluefin tuna growth parameter estimates derived for the seven models described.

Model no.	Model description	μ_{L_∞} (cm)	μ_K/yr	$\sigma_{L_\infty}^2$ (cm^2)	σ_K^2/yr^2	σ_e^2 (cm^2)	t_0 (yr)	LL
1	Fabens	201.1	0.1251			22.96	−0.6884	5183.66
2	Kirkwood and Somers	157.2	0.1892	555.8			−0.2506	5224.31
3	Kirkwood and Somers, with model error	186.9	0.1401	218.8		15.25	−0.5437	5150.86
4	Kirkwood and Somers, with model error and release-length error	186.2	0.1409	238.2		10.92	−0.5396	5151.06
5	Sainsbury	175.2	0.1563	100.7	0.1665E-02		−0.4660	5207.39
6	Sainsbury, with model error	188.3	0.1384	177.8	0.8824E-04	15.00	−0.5620	5150.80
7	Sainsbury, with model error and release-length error	188.0	0.1387	193.0	0.1014E-03	10.56	−0.5601	5150.97

Table 2

Estimates of mean and standard deviation of length-at-age (in cm), based on the parameter estimates for models 1 to 7.

	Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7	
Age	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	38.3	4.8	33.1	5.0	36.3	4.8	36.6	4.5	35.6	8.5	36.6	5.2	36.6	4.9
2	57.4	4.8	54.5	8.2	56.0	5.9	56.0	5.7	55.4	12.2	56.2	6.4	56.1	6.3
3	74.3	4.8	72.2	10.8	73.1	7.0	73.1	6.9	72.3	14.7	73.2	7.5	73.2	7.5
4	89.2	4.8	86.9	13.0	88.0	8.0	88.0	8.0	86.6	16.3	88.1	8.5	88.0	8.6
5	102.4	4.8	99.0	14.8	100.9	8.9	100.9	9.0	98.8	17.3	101.0	9.3	100.9	9.5
6	114.0	4.8	109.0	16.3	112.2	9.7	112.1	9.9	109.3	17.7	112.2	10.0	112.1	10.2
7	124.2	4.8	117.3	17.6	121.9	10.4	121.8	10.6	118.2	17.8	122.0	10.6	121.9	10.8
8	133.3	4.8	124.2	18.6	130.4	11.1	130.3	11.3	125.8	17.6	130.5	11.0	130.4	11.3
9	141.2	4.8	129.9	19.5	137.8	11.6	137.6	11.9	132.4	17.3	138.0	11.4	137.8	11.7
10	148.3	4.8	134.6	20.2	144.2	12.1	144.0	12.4	138.0	16.8	144.4	11.8	144.3	12.0
11	154.5	4.8	138.5	20.8	149.8	12.5	149.6	12.8	142.9	16.3	150.1	12.0	149.9	12.4
12	160.0	4.8	141.7	21.2	154.7	12.9	154.4	13.2	147.1	15.8	155.0	12.3	154.8	12.6
13	164.8	4.8	144.4	21.6	158.9	13.2	158.6	13.5	150.7	15.2	159.2	12.5	159.1	12.8
14	169.1	4.8	146.6	22.0	162.5	13.5	162.2	13.8	153.8	14.7	163.0	12.6	162.8	13.0
15	172.9	4.8	148.4	22.3	165.7	13.7	165.3	14.1	156.5	14.2	166.2	12.8	166.0	13.1
16	176.2	4.8	149.9	22.5	168.5	13.9	168.1	14.3	158.8	13.7	169.0	12.9	168.8	13.3
17	179.1	4.8	151.2	22.7	170.9	14.1	170.5	14.5	160.9	13.3	171.5	13.0	171.3	13.4
18	181.7	4.8	152.2	22.8	173.0	14.3	172.5	14.7	162.6	12.8	173.6	13.1	173.4	13.5
19	184.0	4.8	153.1	23.0	174.8	14.4	174.3	14.8	164.2	12.5	175.5	13.2	175.3	13.6
20	186.0	4.8	153.8	23.1	176.4	14.5	175.9	14.9	165.5	12.1	177.2	13.3	176.9	13.7

tions. The effect of these differences on the mean and standard deviation of length-at-age is shown in Table 2. Despite the differences in parameter estimates, mean length-at-age is virtually identical for all models up to age 7. This allows the calculation of an approximate age-at-release for each observation that should contain little error and that is essentially independent of which set of parameter estimates is used to convert the release length to age. With this information, a presumed age-at-recapture incorporating individual variation can be calculated by adding the presumed age-at-release to the observed period at liberty. A plot of presumed age-at-recapture (calculated using the model 3 parameter estimates) against recapture length is shown in Figure 3.

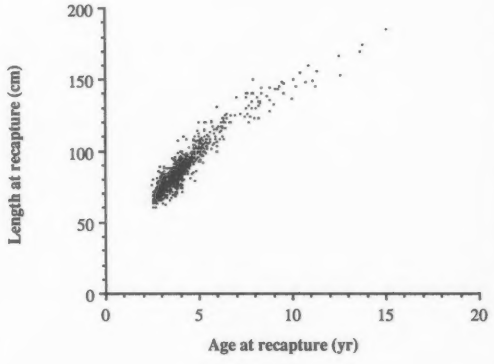

Figure 3

Plot of recapture length against presumed age-at-recapture for tag returns comprising the final data set (n 1736).

Model 1 produced the highest estimate of μ_{L_∞} and the lowest estimate of μ_K. The probable explanation for this is that the estimates are biased by the three observations with the greatest recapture lengths (Fig. 3). Because there is no individual variation in this model, the estimate of L_∞ is forced upward to compensate for these influential observations. In model 2, such observations can be accommodated by individual variation in L_∞; thus the estimate of μ_{L_∞} falls by more than 20% and the estimate of μ_K rises by more than 50%. When a model error term is added (model 3), the differences in relation to model 1 are less dramatic. The addition of release-length-measurement error (model 4) has little effect on the model-3 estimates, with the exception of σ_e^2, which is somewhat lower in model 4. Similar effects of adding model error and release-length-measurement error can be seen in comparisons of the parameter estimates for models 5, 6, and 7.

The estimates of $\sigma_{L_\infty}^2$ are substantially higher for models that assume constant K (models 2, 3, and 4) than for those that assume individual variability in K

Table 3
Values of the 97.5 percentile of the L_∞ distributions derived for models 2–7. These values may be compared with an observed maximum size in the catch of 225 cm.

Model no.	97.5 percentile of the L_∞ distribution (cm)
2	203.4
3	216.0
4	216.5
5	194.8
6	214.4
7	215.2

(models 5, 6, and 7). An approximate consistency test for derived L_∞ distributions is to compare an upper percentile (e.g., 97.5) of the distribution with the observed maximum size in a large sample of the catch (Kirkwood and Somers 1984). The largest southern bluefin ever measured by Japanese researchers during many years of length-frequency sampling is 225 cm (Yukinawa 1970, Shingu 1978). This may be compared with the derived 97.5 percentile of the L_∞ distributions for models 2–7 (Table 3). While by no means a definitive test, the comparisons suggest that the L_∞ distributions derived for models 3, 4, 6, and 7 (models that include model error) are more consistent with the observed maximum length than the distributions derived for models 2 and 5 (models that do not include model error).

The estimate of σ_K^2 for model 5 fell substantially with the addition of model error (models 6 and 7). The value of σ_K^2 for model 7 represents a coefficient of variation of approximately 7%. It should be pointed out here that the log-likelihood surface was very flat with respect to both $\sigma_{L_\infty}^2$ and σ_K^2, i.e., relatively large changes in either parameter resulted in only very small changes in LL. This matter is explored further using simulation techniques.

Model selection

The minimum negative log-likelihood function values given in Table 1 are indicators of the goodness of fit of the models to the data. Model 2 (3 parameters) provided a substantially poorer fit to the data than model 1 (3 parameters) and therefore need not be tested. Also, the inclusion of release-length-measurement error resulted in slightly worse fits to the data, eliminating models 4 and 7 from further consideration. The only likelihood ratio tests that are required are: (1) the null hypothesis (H_0) that model 1 is the correct model against the alternative that model 3 (4 parameters) is correct; (2) the H_0 that model 1 is the correct model against the alternative that model 6 (5 parameters) is correct; and (3) the H_0 that model 3 is the correct model against the alternative that model 6 is correct. H_0 was rejected for both tests (1) and (2) ($P<0.001$), indicating that the more complex models 3 and 6 provide significantly better fits to the data than model 1. For test (3), H_0 was accepted ($P>0.05$), suggesting that the additional complexity of the extra parameter (σ_K^2) in model 6 did not result in a significantly improved fit over model 3. On this basis, model 3 was adopted as the most appropriate model for these data.

Simulations

Assessment of model performance The results of analyses of 100 simulated data sets, produced assuming independence of $L_{\infty i}$ and K_i, are given in Table 4. These suggest that all of the models, with the possible exception of model 2, provide unbiased estimates of μ_{L_∞} and μ_K. This is somewhat surprising in view of the wide range of estimates of these parameters obtained from analyzing real data with the same models (Table 1). In particular, one might have expected, on the basis of analyses of the real data, that models 2 and 5 would have given biased estimates of μ_{L_∞} and μ_K for the simulated data also. The estimates of these parameters obtained from the real data, using the above models, even lie outside the approximate 95% confidence bounds calculated from the simulated data. A possible explanation for this is that the simulated data do not contain all the growth-related features of the real data. Such unaccounted-for structure, if it affected the performance of the models differently, could produce such inconsistencies. This, in fact, was observed in the case of the apparently biased estimates given by model 1 for the real data.

While the simulations indicate that estimates of the mean parameters are relatively unbiased and precise, this is not the case for estimates of their variances. In particular, it is clear that reliable estimates of σ_K^2 cannot be obtained from this data set, since estimates from the simulated data ranged from practically zero to 25% (expressed as the coefficient of variation). This could be due in part to the loss of information on K-variability incurred because of the necessary exclusion from the analyses of fish at liberty for less than 250 days.

The mean values of $\sigma_{L_\infty}^2$ are reasonably consistent with the estimates obtained from the real data. The estimates from models 2, 3, and 4 are positively biased, while those from model 5 are negatively biased. The estimates from model 7 are unbiased, but have a coefficient of variation of 45%. The estimates of σ_e^2 are somewhat less than those obtained from the real data, except in the case of model 1.

Table 4

Results of analyzing 100 simulated data sets generated using model 7, assuming independence of L_∞ and K_i. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

Parameter		Model 1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	189.5	179.9	189.1	190.7	188.1	189.1	189.0
	SE	5.8	5.0	5.0	9.2	5.7	5.9	4.8
	lower c.b.*	178.3	170.0	179.4	172.6	177.0	177.6	179.5
	upper c.b.	200.8	189.8	198.8	208.8	199.2	200.7	198.4
μ_K/yr	mean	0.1372	0.1498	0.1376	0.1362	0.1400	0.1379	0.1378
	SE	0.0071	0.0074	0.0062	0.0093	0.0070	0.0074	0.0061
	lower c.b.	0.1233	0.1352	0.1256	0.1179	0.1263	0.1234	0.1259
	upper c.b.	0.1510	0.1644	0.1497	0.1544	0.1536	0.1525	0.1497
$\sigma_{L_\infty}^2$ (cm^2)	mean		699.2	249.7	288.4	27.1	178.1	186.3
	SE		64.2	44.1	100.5	42.3	93.4	84.8
	lower c.b.		573.4	163.3	91.4	−55.8	−5.0	20.1
	upper c.b.		825.0	336.1	485.4	110.0	361.2	352.4
σ_K^2/yr^2	mean					0.1176 E-2	0.1973 E-3	0.1839 E-3
	SE					0.1509 E-2	0.2503 E-3	0.1476 E-3
	lower c.b.					0.8806 E-3	−0.2932 E-3	−0.1054 E-3
	upper c.b.					0.1472 E-2	0.6879 E-3	0.4733 E-3
σ_e^2 (cm^2)	mean	20.11		11.13	6.67		10.08	6.04
	SE	0.75		0.97	1.11		1.49	1.17
	lower c.b.	18.63		9.22	4.50		7.16	3.75
	upper c.b.	21.59		13.03	8.85		13.00	8.32

*95% confidence bound assuming variables to be normally distributed.

The results of the simulations in which $L_{\infty i}$ and K_i were assumed to be correlated are given in Table 5. These results are essentially identical to those in Table 4; therefore, the assumption of independence does not affect parameter estimation in this instance.

Testing the assumption of normally-distributed l_{2i}

Tests of normality of l_{2i} were performed for 30 combinations of l and t. For each of the combinations, the statistic G (χ^2 distributed with 49 degrees of freedom) and the probability, P, of wrongful rejection of the null hypothesis of normally-distributed l_{2i} were calculated (Table 6). In each case, P is greater than 0.10, and usually substantially so; therefore the null hypothesis is not rejected for any of the combinations of l and t.

Discussion

The estimation of von Bertalanffy growth parameters is one of the more frequently applied analyses in fisheries research. Despite this, the interpretation of the parameter estimates is often ill-founded. This is particularly so with L_∞, which is frequently given the interpretation of maximum possible length. This would be the case only if every fish grew exactly according to the derived model, i.e., there was no model error or individual variation in growth. In reality, the growth of all individual fish will not follow a single von Bertalanffy growth curve exactly; there will be variations among individuals resulting from exogenous (environmental) and endogenous (genetic) effects (Francis 1988). The correct interpretation of L_∞ estimated in the standard way is that it is the average maximum length that would be attained in the population represented by the data being analysed. Models have been proposed in this paper that take explicit account of model error and individual variation in growth, thereby eliminating the need for such interpretations.

Previous estimates of southern bluefin growth parameters have differed substantially (Table 7). The previous estimates of L_∞ obtained from tag-return data are somewhat smaller than the estimate derived using model 1 in this paper. This is possibly because

Table 5

Results of analyzing 100 simulated data sets generated using model 7, assuming correlated $L_{\infty i}$ and K_i pairs. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

Parameter		Model 1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	188.2	178.5	187.6	187.3	186.3	187.1	184.6
	SE	6.6	4.9	5.0	5.1	5.6	6.4	7.8
	lower c.b.*	175.3	168.9	177.7	177.3	175.4	174.6	169.4
	upper c.b.	201.1	188.2	197.5	197.4	197.2	199.6	199.9
μ_K/yr	mean	0.1389	0.1517	0.1395	0.1398	0.1423	0.1404	0.1442
	SE	0.0083	0.0075	0.0065	0.0066	0.0072	0.0080	0.0111
	lower c.b.	0.1226	0.1370	0.1268	0.1269	0.1280	0.1248	0.1224
	upper c.b.	0.1553	0.1664	0.1521	0.1527	0.1563	0.1560	0.1661
$\sigma_{L_\infty}^2$ (cm^2)	mean		688.6	251.3	270.6	38.6	180.9	151.0
	SE		64.3	35.4	36.2	54.2	91.2	94.4
	lower c.b.		562.7	181.9	199.6	−67.6	2.2	−34.0
	upper c.b.		814.6	320.6	341.6	144.7	359.6	336.1
σ_K^2/yr^2	mean					0.1208 E-2	0.2105 E-3	0.4301 E-3
	SE					0.1608 E-3	0.2771 E-3	0.4383 E-3
	lower c.b.					0.8928 E-3	−0.3327 E-3	−0.4290 E-3
	upper c.b.					0.1523 E-2	0.7536 E-3	0.1289 E-2
σ_e^2 (cm^2)	mean	20.33		11.05	6.74		9.99	4.53
	SE	0.79		1.05	1.06		1.74	2.79
	lower c.b.	18.78		8.99	4.66		6.57	−0.95
	upper c.b.	21.88		13.12	8.82		13.41	10.00

*95% confidence bound assuming variables to be normally distributed.

Table 6

Values of the goodness-of-fit test statistic, G (χ^2 distributed with 49 degrees of freedom), and the probability, *P*, of wrongful rejection of the null hypothesis of normally-distributed recapture lengths. Each test consisted of 5000 recapture lengths generated for a specific combination of release length and time-at-liberty. For the purpose of calculating G statistics, the simulated recapture lengths were classified into 50 equiprobable categories.

Release length (cm)		Time-at-liberty (yr) 2	4	6	8	10
50	G	42.02	56.00	58.16	51.68	44.68
	P	0.75	0.22	0.17	0.37	0.65
60	G	57.54	50.86	52.38	38.74	46.84
	P	0.19	0.40	0.34	0.85	0.56
70	G	46.50	37.84	38.92	49.84	42.44
	P	0.58	0.88	0.85	0.44	0.73
80	G	56.68	45.62	60.92	40.42	48.58
	P	0.21	0.61	0.12	0.80	0.49
90	G	51.58	56.70	53.94	45.42	58.86
	P	0.37	0.21	0.29	0.62	0.16
100	G	54.96	45.70	46.70	31.94	43.78
	P	0.26	0.61	0.57	0.97	0.68

previous studies did not restrict the data to those observations where release length was at least 50 cm and time at liberty at least 250 days (except Kirkwood 1983 in the case of the latter restriction).

The estimates of L_∞ and K based on length-frequency data only (Shingu 1970, Hynd and Lucas 1974, Kirkwood 1983) and those based on scale (Yukinawa 1970) and otolith readings (Thorogood 1986) must be treated with caution because they were estimated from samples which consisted of no, or very few, larger fish (in the case of length-frequency data, modes are rarely visible beyond 100 cm). As discussed by Knight (1968), this almost inevitably leads to biased estimates of the growth parameters.

The analyses of both real and simulated data indicate that biased parameter estimates may result if model error is ignored. In addition, the incorporation of

Table 7
Southern bluefin tuna growth parameter estimates derived by other workers.

Source	Method	L_∞ (cm)	K/yr	t_0 (yr)	n
Shingu (1970) (data from Robins 1963)	Length-frequency	222.5	0.140	0.011	?
Shingu (1970)	Tag return	187.4	0.149	0.021	?
Yukinawa (1970)	Scales	219.7	0.135	0.040	1025
Hynd and Lucas (1974)	Length-frequency	220.0	0.150		?
Murphy (1977)	Tag return	180.8	0.146	−0.011	2578
Hearn (unpubl.)	Tag return	178.6	0.117	−0.010	629
Kirkwood (1983)	Tag return	185.3	0.155		794
	Tag return*	209.0	0.125		794
	Length-frequency	184.2	0.166	−0.036	77
	Length-frequency*	214.8	0.133	−0.095	77
	Tag return and length-frequency	184.4	0.157	−0.215	794+77
	Tag return and length-frequency*	207.6	0.128	−0.394	794+77
Thorogood (1986)	Otoliths	261.3	0.108	−0.157	~480

*Time-at-liberty and/or age assumed to be the dependent variable.

model error to both the Kirkwood and Somers model and the Sainsbury model resulted in significantly better fits to the data. This suggests that growth models that include individual variability should, if possible, include model error in the estimation procedure.

Release-length-measurement error did not prove to be a significant source of error in this case. However, its effect should, if possible, be tested in tag-recapture growth studies and, if significant, incorporated into the model as shown in this paper. This will be essential if negative length increments are included in the data set being analysed.

Sainsbury (1980) showed that an underestimate of mean K can result if substantial individual variability in K is present but ignored. There are a number of indications from southern bluefin data that the level of individual variability in K is not substantial. First, there is virtually no difference in estimates of μ_{L_∞} and μ_K between models 3 and 6 and between models 4 and 7. (The only difference in the models in each case is that both the latter models incorporate individual variability in K.) If the real level of individual variability in K was substantial, we might expect, on the basis of Sainsbury's (1980) observation, that models 3 and 4 would have given overestimates of μ_{L_∞} and underestimates of μ_K compared with models 6 and 7. Second, analyses of length-frequency modes suggest that the variance of length-at-age increases with increasing age (W.S. Hearn, CSIRO Div. Fish., GPO Box 1538, Hobart 7001, Aust., pers. commun.). This, as Sainsbury (1980) notes, is more the rule than the exception in fish populations, and is indicative of variation in L_∞ having the dominant effect on overall variation in length-at-age. Third, modes are clearly visible in the length-frequency data for at least the first four age-classes (Kirkwood 1983). Majkowski et al. (1987) give a general condition for the visual or statistical separability of length-frequency modes as $|\mu_i - \mu_{i-1}| < 2\min(\sigma_i, \sigma_{i+1})$, where μ_i and σ_i are the mean length and its standard deviation, respectively, of age-class i. Applying this condition to the mean-length and standard-deviation-at-age data given in Table 2, we find that only for models 3 and 4 (no variation in K) and models 6 and 7 ($\sigma_K/\mu_K = 0.07$) is the condition satisfied for separating age-classes 3 and 4. On this basis, we could conclude that the visibility of at least four modes in the length-frequency data would preclude levels of K variability much greater than those derived for models 6 and 7.

The problem of selecting the most appropriate model for use in stock assessment was addressed, using likelihood ratio tests. These indicated that model 1 was inadequate, and that a significantly better description of the data was provided by incorporating individual variation in L_∞ (model 3). However, the incorporation of individual variation in K or release-length-measurement error could not be justified.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Natural Mortality and Movement Rates from Tagging Experiments

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Abstract.–Two models were fit to data from four experiments in which tagged southern bluefin tuna *Thunnus maccoyii* were released in Australian coastal waters and recaptured in the Australian surface fisheries and the Japanese longline fishery. The principal objective of the analysis was to estimate the instantaneous rate of natural mortality (M). Movement rates and catchability coefficients were also estimated using the second model. The first model (HSH) was fit to exact recapture times assuming, *inter alia*, that the tagged population was extinct at the time of the last tag return. The second model (SE) was fit to grouped data classified by two release fisheries and three recapture fisheries, explicitly incorporating movement between the geographically separated release fisheries and permanent emigration from the release fisheries into the Japanese longline fishery. Using the HSH model, estimates of M ranged from 0.20 to 0.42/year for the different experiments if full reporting of recaptured tags was assumed. The estimates decreased slightly as assumed reporting rate was decreased. The SE model yielded estimates of M ranging from 0.20 to 0.23/year with M constrained to be equal in each of the recapture fisheries. Unconstrained-M estimates were obtained which suggested higher levels of natural mortality in the release fisheries; however, these estimates were considered unreliable because of their large standard errors and high degree of confounding with other parameters of the model. Simulation trials indicated that input parameters used to generate simulated tag-return data sets could be accurately retrieved using the SE model. However, the HSH model produced positively biased estimates of M because of the low level of apparent fishing mortality in the Japanese longline fishery.

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The rate at which members of a fish population die from causes other than fishing, the so-called instantaneous rate of natural mortality (M), has a large bearing on the population and fishery dynamics of an exploited species. Natural death is rarely directly observable in fish populations, making M notoriously difficult to estimate, and much attention has been given over the years to devising experimental and statistical techniques to do so. The experimental technique most frequently used is tagging and recapture, the object of which, as stated by Beverton and Holt (1957), is "...to set up and examine the properties of an 'experimental' population of marked fish in which certain parameters that would be difficult or impossible to estimate in the 'natural' population can be determined with some accuracy".

A variety of statistical techniques has been developed to estimate M and other parameters from tagging experiments. One of the simplest is that of Gulland (1955), who derived maximum likelihood estimators for M and the fishing mortality rate (F) (both assumed constant over time) for a completed tagging experiment (i.e., one in which no tagged fish remain alive at the time of the last tag recapture). Hearn et al. (1987) generalized the Gulland (1955) method by allowing F to vary with time. Other models based on log-linear regression (Sandland 1982) or maximum likelihood estimation (Seber 1973, Wetherall 1982) normally require M and F to be constant; however, some of the more sophisticated methods allow F to vary with time as a function of fishing effort or catch (e.g., Lucas 1975, Kleiber et al. 1987). As an extension of these single-fishery models, Sibert (1984) developed a two-fishery model in which estimates of M, F, and the rates of movement between the fisheries could be obtained.

The southern bluefin tuna *Thunnus maccoyii* for many years has been the subject of an important fishery in southern Australian waters, where juveniles form surface schools and are captured principally by pole-and-line and purse-seine gears. In addition, a large fleet of Japanese longliners has targeted the adults in the higher, southern latitudes of the Indian, Southern, Pacific, and Atlantic Oceans since 1952.

Tagging experiments conducted by the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) have demonstrated that these fisheries exploit a common stock (Hampton 1989), and that there is considerable movement of juvenile fish between fishing grounds off the south coast of western Australia (WA), in the Great Australian Bight off south Australia (SA), and off the south coast of New South Wales (NSW). Throughout the juvenile phase, southern bluefin move away from the Australian coast and subsequently become recruited to the Japanese longline fishery (Fig. 1).

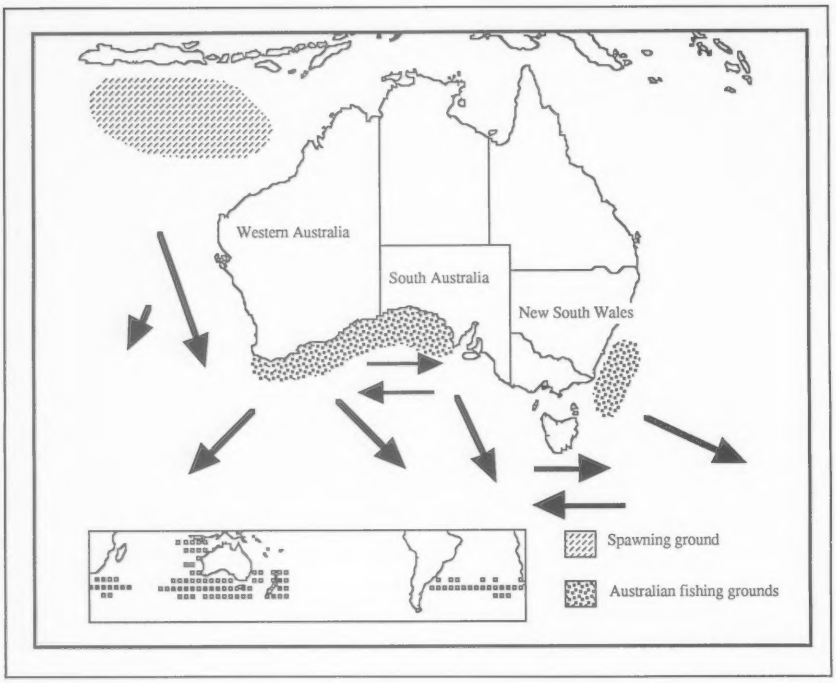

Figure 1
Geographical distribution of the Australian and Japanese (inset) southern bluefin tuna fisheries. Arrows indicate movement of fish in and away from Australian coastal waters. Black squares on the inset map indicate areas of higher Japanese catch.

During the 1980s, scientists became concerned that the fishery was being overexploited, and recent stock assessments have indicated the possibility that a decline in recruitment to the surface fishery could have occurred (Caton et al. 1990). These stock assessments have been based almost exclusively on cohort analysis (Gulland 1965) and other age-structured models, all of which require an estimate of M.

Despite its importance in stock assessment, the natural mortality rate of southern bluefin tuna has never been investigated in detail. Hayashi et al. (1969) considered a value of 0.2/year to be appropriate, based on a somewhat *ad hoc* comparison with growth parameter estimates. This value of M has been preferred in most stock assessments, although a range of values has also been used at various times (e.g., Hampton et al. 1984, Hampton and Majkowski 1986). More recently, the application of the Hearn et al. (1987) method to southern bluefin tagging data suggested that M could be somewhat higher than the "traditional" value of 0.2/year, possibly in excess of 0.4/year. However, the authors acknowledged that this was probably an overestimate because of likely non-compliance with various assumptions.

In this paper, selected southern bluefin tuna tagging experiments are analysed for the purpose of deriving estimates of M consistent with the tagging data. The Hearn et al. (1987) model (referred to as the HSH model) and an extension of the Sibert (1984) model (referred to as the SE model), which also provides estimates of movement rates between geographically separated fisheries and catchability coefficients, are applied. These models are tested using a simulation model that reflects characteristics of the southern bluefin population and fisheries.

Tagging data

Between 1959 and 1984, the CSIRO supervised the tagging of more than 60,000 southern bluefin tuna, mostly aged 2–4 years, of which approximately 12,000 have been recaptured and the tags returned. From these data, four tagging experiments from which no further returns are expected were defined (Table 1). Although other groupings of the tagging data are possible, the experiments were defined in this way so that they represent reasonably homogeneous groups in terms of release area, size of tagged fish, time period of release, fishing method, and tagging personnel involved. All fish were double-tagged using methods described by Williams (1982). All returns from these experiments were included in the analyses, with best estimates of recapture times (normally the midpoint of the fishing

Table 1

Southern bluefin tuna double-tagging experiments off Australia. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Experiment no.	Area	Years	Carried out by	Fishing method	No. released	No. recovered
1	NSW	1963–70	CSIRO	Pole-and-line	2770	433
2	NSW	1963–70	Fishermen under contract to CSIRO	Troll	9513	4205
3	SA	1964–69	CSIRO	Pole-and-line	7328	1276
4	WA	1963–67	CSIRO	Pole-and-line	12826	563

season) used for those returns where an exact recapture time was not available. The numbers of such returns were relatively few (experiment 1: 27, experiment 2: 114, experiment 3: 47, experiment 4: 35.

Methods of analysis

General assumptions of tagging experiments

Before describing the analytical methods used in this study, some discussion of general assumptions required for the estimation of mortality rates from tag-return data is warranted. These assumptions relate mostly to accounting for all forms of tag loss. In particular, tag losses due to tag shedding, tagging-induced mortality (e.g., through infection, or increasing the probability of predation or capture), and non-reporting of recovered tags must be absent or accounted for. This is frequently achieved by carrying out separate experiments to estimate parameters of models that describe these processes, e.g., double-tagging experiments to estimate tag-shedding rates, holding-tank experiments to test for tagging-induced mortality, and tag-seeding experiments to estimate the proportion of recovered tags that are returned to the tagging authority. The approach taken in this paper was to account for tag shedding using estimates derived by Hampton and Kirkwood (1990), assume tagging-induced mortality to be absent on the basis of various field observations, and repeat the parameter estimations over a range of plausible tag-reporting rates.

In addition to assumptions regarding tag loss, for analyses that include parameters or data relating to the recapture fishery, it is necessary to assume that the tagged and untagged populations are equally vulnerable to capture from the moment of release. Compliance with these and other assumptions for the present application are discussed in a later section.

The HSH model

In addition to the assumptions regarding tag loss, it is assumed here that all recapture times are accurately known, M is constant, the experiment is completed (i.e., no tagged fish remain alive at the time of the last tag recapture), and all tagged fish remain vulnerable to the fishery through a possibly variable but ultimately non-zero level of fishing mortality. Cessation of fishing would violate the assumption of completion, while permanent emigration of tagged fish away from the fishery would violate the assumption of complete vulnerability.

Let N_0 fish be released and n recaptures recorded at times $t_1 < t_2 < \ldots t_n$ after release. If the above assumptions are satisfied, the natural mortality rate estimator, $\hat{M}$, is obtained by solving the equation, derived by Hearn et al. (1987),

$$N_0 - \sum_{i=1}^{n} e^{Mt_i} = 0, \qquad (1)$$

using a numerical method such as the Newton-Raphson (Courant 1937).

Tag shedding is accounted for by introducing for each return a correction factor, w_i, which is the probability of a tagged fish retaining at least one tag at time t_i. For double-tagging experiments,

$$w_i = Q(t_i)\,[2 - Q(t_i)], \qquad (2)$$

where $Q(t_i)$ is the probability of a tag being retained at time t_i after release. Tag-shedding models have been fit to double-tagging data for each of the experiments (Hampton and Kirkwood 1990), the results of which are given in Table 2.

The tag-shedding correction is incorporated into Equation (1) as follows:

$$N_0 - \sum_{i=1}^{n} \frac{e^{Mt_i}}{w_i} = 0. \qquad (3)$$

Similarly, the non-reporting of recaptured tagged fish can be allowed for if the fraction, R, of recaptured tagged fish actually reported to the tagging authority is known or assumed. Equation (3) then becomes

Table 2
Tag-shedding models and parameter estimates (from Hampton and Kirkwood 1990) used in the estimation of natural mortality rate and related parameters of southern bluefin tuna.

Experiment	Tag-shedding model	Parameter estimates λ	b	ρ
1	$Q(t) = \rho e^{-\lambda t}$	0.29		0.93
1	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^b$	1.00	0.26	
2	$Q(t) = \rho e^{-\lambda t}$	0.17		0.98
3	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^b$	0.78	0.26	
4	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^b$	1.04	0.36	

$$N_0 R - \sum_{i=1}^{n} \frac{e^{M t_i}}{w_i} = 0.$$

If there is a long-term mortality associated with bearing tags, this will be incorporated into $\hat{M}$ and be indistinguishable from it. An initial mortality due to tagging simply reduces the effective number of releases; if known, it can be included in the model in an identical fashion to R.

As discussed in Hearn et al. (1987), an estimate of the standard error of $\hat{M}$ is not available by conventional means because the estimate is conditional on the distribution of the data t_i. There is also no guarantee that the estimator is unbiased. A statistical tool that is commonly used in applied statistics both to reduce the bias of an estimator and to provide an approximate standard error is the jackknife (Cox and Hinkley 1974). This technique is not described in detail here; suffice to say that it is based on N_0 separate estimates of M that are obtained by removing, in turn, each tagged fish (whether recaptured or not) from the data. The mean of these estimates is the jackknife estimate of M, and their standard error is the jackknife estimate of the standard error of $\hat{M}$.

The SE model: An extension of the Sibert model

This model, unlike the HSH model, is fit to data grouped into time intervals, rather than individual, exact recapture times. In common with traditional single-release tag-attrition models (as described in detail, for example, in Seber 1973 and Wetherall 1982) that have been used extensively in the analysis of mark-recapture data, the SE model is based on classical population dynamics theory, as embodied in the Baranov catch equation (Baranov 1918).

The SE model extends the work of Sibert (1984), who developed a method of analyzing a tagging experiment in which tagged fish are released (not necessarily simultaneously) into two geographically separate fisheries that interact through the movement of fish. Sibert accomplished this basically by adding a spatial dimension and incorporating movement rates into the Baranov catch equation. Tag returns and catch or effort from the two fisheries, by time interval, form the observations to which the model is fit, yielding estimates of movement rates between the two fisheries, and estimates of M, catchability coefficient (when effort is used), and average population size (when catch is used) for each fishery. Recently, Hilborn (1990) developed a model similar to Sibert's in terms of estimation of movement rates; however, natural mortality rate is not specified in the population dynamics and therefore cannot be estimated using the Hilborn model.

To facilitate analyses of southern bluefin tagging experiments, Sibert's two-fishery model is extended in this paper to incorporate a third recapture fishery (the Japanese longline fishery). It is now assumed that there is movement of tagged fish from fisheries 1 and 2 (the release fisheries) into fishery 3. Movement between fisheries 1 and 2 can take place in both directions, but movement into fishery 3 is assumed to be permanent, i.e., there is no possibility of movement back to either fishery 1 or 2 once a fish has moved to fishery 3. This restriction of the model is adopted to avoid the necessity of estimating two additional movement parameters about which little information is available in the absence of releases into fishery 3 (large-scale tagging in the longline fishery is not feasible for southern bluefin tuna). However, this assumption is consistent with the known migratory behavior and the age composition of catches of southern bluefin from the Australian and Japanese fisheries (Hampton 1989).

In addition to the normal assumptions regarding tag loss, equal vulnerability of tagged and untagged fish must be assumed since catch and/or effort statistics are required for the analysis. It is also assumed, for simplicity, that M is constant over time within recapture fisheries.

Model derivation Following release, the tagged fish fall into six categories: the numbers released into fishery 1 that are at large in fishery 1 (N_{11}), fishery 2 (N_{12}), and fishery 3 (N_{13}), and the numbers released into fishery 2 that are at large in fishery 1 (N_{21}),

fishery 2 (N_{22}), and fishery 3 (N_{23}). The way in which these quantities change over time can be represented by six simultaneous differential equations (assuming, for the moment, that tag losses due to tag shedding, tag-induced mortality, and non-reporting are absent):

$$\frac{dN_{11}}{dt} = -(M_1 + F_1 + T_{12})N_{11} + T_{21}N_{12} \qquad (\text{at } t = 0,\ N_{11} = N_{01})$$

$$\frac{dN_{12}}{dt} = -(M_2 + F_2 + T_{21})N_{12} + T_{12}N_{11} \qquad (\text{at } t = 0,\ N_{12} = 0),$$

$$\frac{dN_{13}}{dt} = -(M_3 + F_3)N_{13} + T_{13}N_{11} + T_{23}N_{12} \qquad (\text{at } t = 0,\ N_{13} = 0),$$

$$\frac{dN_{21}}{dt} = -(M_1 + F_1 + T_{12})N_{21} + T_{21}N_{22} \qquad (\text{at } t = 0,\ N_{21} = 0),$$

$$\frac{dN_{22}}{dt} = -(M_2 + F_2 + T_{21})N_{22} + T_{12}N_{21} \qquad (\text{at } t = 0,\ N_{22} = N_{02}),$$

$$\frac{dN_{23}}{dt} = -(M_3 + F_3)N_{23} + T_{23}N_{22} + T_{13}N_{21} \qquad (\text{at } t = 0,\ N_{23} = 0), \qquad (4)$$

where N_{01} and N_{02} are the number of releases into the two fisheries, M_1, M_2, and M_3 are the rates of natural mortality operating in the three fisheries, F_1, F_2, and F_3 are the rates of fishing mortality specific to the three fisheries (assumed, for the moment, to be constant over time), and T_{12}, T_{13}, T_{21}, and T_{23} are movement rates (the first subscript denoting the donor fishery and the second subscript denoting the recipient fishery).

Tag returns from the three fisheries can be classified in a similar fashion to numbers at large, i.e., r_{11}, r_{12}, and r_{13} are the numbers of returns of fish released in fishery 1 that are recaptured in fisheries 1, 2, and 3, respectively, and r_{21}, r_{22}, and r_{23} are the numbers of returns of fish released in fishery 2 that are recaptured in fisheries 1, 2, and 3, respectively. The estimated rates of return in these categories can be written as:

$$\frac{d\hat{r}_{11}}{dt} = F_1N_{11},$$

$$\frac{d\hat{r}_{12}}{dt} = F_2N_{12},$$

$$\frac{d\hat{r}_{13}}{dt} = F_3N_{13},$$

$$\frac{d\hat{r}_{21}}{dt} = F_1N_{21},$$

$$\frac{d\hat{r}_{22}}{dt} = F_2N_{22},$$

and

$$\frac{d\hat{r}_{23}}{dt} = F_3N_{23}. \qquad (5)$$

Equations (4) and (5) are solved by integrating between times t and $t+\Delta t$. For ease of notation, define $A_1 = M_1 + F_1 + T_{12} + T_{13}$, $A_2 = M_2 + F_2 + T_{21} + T_{23}$, and $A_3 = M_3 + F_3$. Integrating Equations (4) is accomplished by applying a decoupling transformation (see Sibert 1984 for details) and results in the following set of delay-difference equations,

$$N_{11(t+\Delta t)} = \frac{1}{1+ab}\{a[bN_{11(t)} + N_{12(t)}]\, e^{-u\Delta t} + [N_{11(t)} - aN_{12(t)}]\, e^{-v\Delta t}\},$$

$$N_{12(t+\Delta t)} = \frac{1}{1+ab}\{[bN_{11(t)} + N_{12(t)}]\, e^{-u\Delta t} - b[N_{11(t)} - aN_{12(t)}]\, e^{-v\Delta t}\},$$

$$N_{13(t+\Delta t)} = N_{13(t)}\, e^{-A_3\Delta t} + \frac{T_{13}}{A_1-A_3} N_{11(t)}\,[e^{-A_3\Delta t} - e^{-A_1\Delta t}] + \frac{T_{23}}{A_2-A_3} N_{12(t)}\,[e^{-A_3\Delta t} - e^{-A_2\Delta t}],$$

$$N_{21(t+\Delta t)} = \frac{1}{1+ab}\{a[N_{22(t)} + bN_{21(t)}]\, e^{-u\Delta t} + [N_{22(t)} - aN_{22(t)}]\, e^{-v\Delta t}\},$$

$$N_{22(t+\Delta t)} = \frac{1}{1+ab}\{[N_{22(t)} + bN_{21(t)}]\, e^{-u\Delta t} - b[N_{21(t)} - aN_{22(t)}]\, e^{-v\Delta t}\},$$

and

$$N_{23(t+\Delta t)} = N_{23(t)}\, e^{-A_3\Delta t} + \frac{T_{23}}{A_2-A_3} N_{22(t)}\,[e^{-A_3\Delta t} - e^{-A_2\Delta t}] + \frac{T_{13}}{A_1-A_3} N_{21(t)}\,[e^{-A_3\Delta t} - e^{-A_1\Delta t}], \qquad (6)$$

where a and b, the coefficients of the decoupling transformation, are roots of two quadratic equations,

$$T_{12}a^2 - (A_2-A_1)a - T_{21} = 0, \qquad T_{21}b^2 - (A_2-A_1)b - T_{12} = 0,$$

and

$$v = \frac{A_1+bT_{21}+abA_2+aT_{12}}{1+ab}, \qquad u = \frac{A_2-aT_{12}+abA_1-bT_{21}}{1+ab}.$$

Substituting Equations (6) into Equations (5) and integrating, the estimated numbers of tagged fish of each category recaptured between times t and $t+\Delta t$ are obtained:

$$\hat{r}_{11(t)} = \frac{R_1F_1}{1+ab}\left\{a\left[\frac{bN_{11(t)}+N_{12(t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{11(t)}-aN_{12(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{12(t)} = \frac{R_2F_2}{1+ab}\left\{\left[\frac{bN_{11(t)}+N_{12(t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{11(t)}-aN_{12(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{13(t)} = R_3F_3\left\{\left[\frac{T_{13}}{A_1-A_3}N_{11(t)}+N_{13(t)}\right]\frac{(1-e^{-A_3\Delta t})}{A_3} - \frac{T_{13}}{A_1-A_3}N_{11(t)}\frac{(1-e^{-A_1\Delta t})}{A_1}\right\},$$

$$\hat{r}_{21(t)} = \frac{R_1F_1}{1+ab}\left\{a\left[\frac{N_{22(t)}+bN_{21(t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{21(t)}-aN_{22(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{22(t)} = \frac{R_2F_2}{1+ab}\left\{\left[\frac{N_{22(t)}+bN_{21(t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{21(t)}-aN_{22(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

and

$$\hat{r}_{23(t)} = R_3F_3\left\{\left[\frac{T_{23}}{A_2-A_3}N_{22(t)}+N_{23(t)}\right]\frac{(1-e^{-A_3\Delta t})}{A_3} - \frac{T_{23}}{A_2-A_3}N_{22(t)}\frac{(1-e^{-A_2\Delta t})}{A_2}\right\}. \quad (7)$$

Equations (6) and (7) describe the dynamics of tagged fish as a function of the parameters M_1, M_2, M_3, F_1, F_2, F_3, T_{12}, T_{13}, T_{21}, and T_{23}. Fishery-specific reporting rates, R_1, R_2, and R_3, have been introduced and are assumed known. The tag-shedding correction factor, w_t, (Eq. 2) can be introduced in a similar fashion to R (i.e., as a multiplier of F). Note that w_t now refers to the probability of retaining at least one tag at the midpoint of period $t + \Delta t$ and may differ according to fishery of release.

In practice, it is likely that the Fs will vary with time. If catch or effort data are available by time period (indexed by i), F_1, F_2, and F_3 can be reparameterized as

$$F_{1i} = q_1f_{1i} \sim \frac{C_{1i}}{P_1},$$

$$F_{2i} = q_2f_{2i} \sim \frac{C_{2i}}{P_2},$$

$$F_{3i} = q_3f_{3i} \sim \frac{C_{3i}}{P_3}, \quad (8)$$

where q_1, q_2, and q_3 are catchability coefficients for the three fisheries, f_{1i}, f_{2i}, and f_{3i} are the fishing efforts in the three fisheries in time period i, P_1, P_2, and P_3 are mean population sizes available to the three fisheries over the course of the tagging experiment, and C_{1i}, C_{2i}, and C_{3i} are catches in the three fisheries during period i (expressed in the same units as P). Variable F can now be accommodated without the addition of extra parameters to the model. This, as noted above, involves the assumption that the tagged and untagged fish are equally vulnerable from the moment of release. The choice of which parameterization to use will ultimately depend on the data available and how one views the relationship between catch, effort, catchability, and population size. In fisheries for surface schooling tunas, effective effort is extremely difficult to quantify, and no such estimates are available for the southern bluefin fisheries. For this reason, I have preferred the parameterization using catch in this paper, although for ease of presentation of simulation results, this has been done by assuming the catch to be an index of effective effort and estimates of q, rather than P, obtained. (By so doing, P is in fact the reciprocal of q.) Note that Equations (8) are approximations in the case of catch data, and require that the populations be close to equilibrium for unbiased estimates to be obtained.

Sibert (1984) used a least-squares technique to obtain estimates of the various parameters for the two-fishery model, and employed a square-root transformation as a weighting scheme for observations within the four tag-recovery categories. Several methods of weighting the four individual sums of squares were also tested. Difficulties can arise in choosing the most appropriate weighting scheme, both for observations within and between return categories. These problems can be avoided by using a maximum-likelihood technique based on multinomial probabilities (Seber 1973). Here, a likelihood function can be constructed for each fishery of tag release, e.g., for releases into fishery 1,

$$f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) = \frac{N_{01}!\,(1-Pr_1)^{N_{01}-n_1}\prod_{i=1}^{k}\{p_{11(i)}^{r_{11(i)}}\,p_{12(i)}^{r_{12(i)}}\,p_{13(i)}^{r_{13(i)}}\}}{\left\{\prod_{i=1}^{k} r_{11(i)}!\,r_{12(i)}!\,r_{13(i)}!\right\}(N_{01}-n_1)!},$$

where n_1 is the total number of returns from fishery 1 releases, up to and including period k, $p_{11(i)}$ is the probability of recovery in fishery 1 during period i ($p_{11(i)} = \frac{\hat{r}_{11(i)}}{N_{01}}$), $p_{12(i)}$ is the probability of recovery in fishery 2 during

period i ($p_{12(i)} = \frac{\hat{r}_{12(i)}}{N_{01}}$), $p_{13(i)}$ is the probability of recovery in fishery 3 during period i ($p_{13(i)} = \frac{\hat{r}_{13(i)}}{N_{01}}$), and

$$Pr_1 = \sum_{i=1}^{k} p_{11(i)} + p_{12(i)} + p_{13(i)}.$$

An equivalent function, $f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})$ can be written for releases into fishery 2. Estimates of parameters may then be found by minimizing

$$L = -\log_e [f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) \cdot f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})]$$

with an estimate of the variance-covariance matrix found using the inverse-Hessian method (Bard 1974).

Simulation trials using the model described below showed that unbiased results are obtained using the maximum-likelihood technique, whereas unbiased results could not be guaranteed with the least-squares approach. In the applications of the SE method presented here, the maximum-likelihood estimation technique is used.

Simulation model

In order to examine the behavior of the HSH and SE estimates, a simulation model was developed. The simulation model determines the fate of each tagged fish released into the two fisheries in a probabilistic fashion. For the moment, consider only releases into fishery 1. During the first time period after release, a tagged fish will either:

(i) be recaptured in fishery 1;
(ii) die from natural causes in fishery 1;
(iii) survive in fishery 1 to the end of the first period and then be subject to all possibilities in the next time period;
(iv) migrate to fishery 2 at time $x<1$;
(v) migrate to fishery 3 at time $x<1$;
(vi) given (iv), be recaptured in fishery 2 at time y ($x<y<1$);
(vii) given (iv), die from natural causes in fishery 2 at time y ($x<y<1$);
(viii) given (iv), survive in fishery 2 until the end of time period 1 and then be subject to possibilities (vi) through (x) in the next time period;
(ix) given (iv), migrate back to fishery 1 at time y ($x<y<1$) and then be subject to all possibilities for the remainder of time period 1;
(x) given (iv), migrate to fishery 3 at time y ($x<y<1$) and then be subject to possibilities (xi) through (xiii) in fishery 3 for the remainder of time period 1;
(xi) given (v), be recaptured in fishery 3 at time y ($x<y<1$);
(xii) given (v), die from natural causes in fishery 3 at time y ($x<y<1$);
(xiii) given (v), survive in fishery 3 until the end of time period 1 and then be subject to possibilities (xi) through (xiii) in the next time period.

The probabilities of each of these events occurring are (omitting, for convenience, the time subscript):

$$P(i) = [1-e^{-A_1}]\frac{F_1}{A_1},$$

$$P(ii) = [1-e^{-A_1}]\frac{M_1}{A_1},$$

$$P(iii) = e^{-A_1},$$

$$P(iv) = [1-e^{-A_1}]\frac{T_{12}}{A_1},$$

$$P(v) = [1-e^{-A_1}]\frac{T_{13}}{A_1},$$

$$P(vi) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{F_2}{A_2},$$

$$P(vii) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{M_2}{A_2},$$

$$P(viii) = P(iv) \cdot e^{-A_2(1-x)},$$

$$P(ix) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{T_{21}}{A_2},$$

$$P(x) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{T_{23}}{A_2},$$

$$P(xi) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{F_3}{A_3},$$

$$P(xii) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{M_3}{A_3},$$

and

$$P(xiii) = P(v) \cdot e^{-A_3(1-x)}.$$

F_1, F_2, and F_3 may be allowed to vary by specifying a constant q or P and dependent f or C (as per Equations 8). An identical process deals with releases into fishery 2.

To determine which of the possible outcomes (i) to (v) first befalls a tagged fish, a pseudorandom number, α, uniformly distributed on [0,1] is generated using a computer subroutine (e.g., subroutine URAND given in Forsythe et al. 1977:245). If $\alpha < P(i)$, outcome (i) is chosen; if $P(i) < \alpha < [P(i) + P(ii)]$, outcome (ii) is chosen; if $[P(i) + P(ii)] < \alpha < [P(i) + P(ii) + P(iii)]$, outcome (iii) is chosen; and so on. Additional pseudorandom numbers are generated and further tests relating to outcomes (vi) to (xiii) applied as necessary until the fish is deemed to have been recaptured, died naturally, or survived to the end of the experiment. When the fates of all tagged fish released into both fisheries are determined in this way, the six tag-return vectors, r_{11}, r_{12}, r_{13}, r_{21}, r_{22}, and r_{23} are established. The SE model can then be fit to these data and the estimated parameter values compared with the "real" values input to the simulation model. The HSH model can be similarly tested, with exact recapture times within the determined period of capture simulated by randomly sampling from a truncated exponential distribution (truncated at one year in this case) as shown in Hearn et al. (1987).

Results

HSH model

The jackknife estimates of M and their standard errors obtained by fitting the HSH model to data from experiments 1–4 are given in Table 3. If full reporting of tags is assumed, the estimates of M range from just less than 0.2/year to just more than 0.4/year; the estimates decrease slightly as reporting rate decreases.

It is clear that the tag-shedding model used to weight the returns has a large bearing on the estimate of M obtained. For experiment 2, the best fitting tag-shedding model (constant shedding rate) predicts a very low probability of tag retention after long periods at liberty (Hampton and Kirkwood 1990). Therefore, those returns from the Japanese fishery at liberty for longer than, say, 6 years will receive large weight in the analysis using the HSH method; this is one of the main reasons for the relatively low estimate of M (0.2275/year for a reporting rate of 1.0). In contrast, a decreasing tag-shedding rate model provided the best fit to the double-tagging data from experiments 3 and 4. Here, there is little change in the probability of tag retention after about 3 or 4 years at liberty (Hampton and Kirkwood 1990). All returns after this time will, then, receive similar weight from the tag-shedding model; accordingly, relatively high estimates of M are obtained for experiments 3 and 4 (0.4165/year and 0.4163/year, respectively, for a reporting rate of 1.0). The most direct test of the effect of the different tag-shedding models is the application of both constant and decreasing shedding-rate models to the analysis of experiment 1 (these tag-shedding models provided equally good fits to experiment 1 double-tagging data, and could not be distinguished on the statistical criterion used by Hampton and Kirkwood 1990). Here, the estimate of M obtained when the constant shedding-rate model was used

Table 3

Estimates of the rate of natural mortality (M) and their standard errors (SE) for different reporting rates (R) obtained from fitting the HSH model to data from experiments 1–4 (see Table 1 for descriptions). Separate estimates are given for two tag-shedding models derived for experiment 1. All estimates are in units per year.

	Experiment 1				Experiment 2		Experiment 3		Experiment 4	
	Constant shedding rate		Decreasing shedding rate		Constant shedding rate		Decreasing shedding rate		Decreasing shedding rate	
R	M	SE	M	SE	M	SE	M	SE	M	SE
1.0	0.1987	0.0681	0.4038	0.0634	0.2275	0.1740	0.4165	0.0860	0.4163	0.0646
0.9	0.1896	0.0674	0.3941	0.0625	0.2239	0.1604	0.4091	0.0815	0.4098	0.0633
0.8	0.1792	0.0665	0.3827	0.0613	0.2194	0.1420	0.4002	0.0763	0.4023	0.0619
0.7	0.1669	0.0654	0.3693	0.0599	0.2122	0.1158	0.3891	0.0702	0.3937	0.0601
0.6	0.1519	0.0640	0.3527	0.0580	0.1965	0.0733	0.3748	0.0628	0.3835	0.0581
0.5	0.1330	0.0620	0.3312	0.0553	0.1148	0.0205	0.3549	0.0538	0.3710	0.0556

(0.1987/year for a reporting rate of 1.0) is less than half the estimate obtained when the decreasing shedding-rate model was used (0.4038/year for a reporting rate of 1.0).

SE model

The SE model was fit to the tag-return data from experiments 2 and 3 (analysis A) and experiments 2 and 4 (analysis B). These data, along with the catch data used to parameterize Fs, are shown in Tables 4 and 5, respectively. For analysis A, returns from the NSW fishery (fishery 1) were defined by recapture positions east of 145°E. SA fishery (fishery 2) returns were defined by recapture positions west of 145°E. No returns from these experiments were recorded in WA (defined for these purposes as west of 125°E) as commercial tuna fishing in WA did not begin until 1969. For analysis B, there is a slight complicating factor in that southern bluefin were tagged in WA before substantial commercial fishing began in 1969; the majority of the few returns recorded in WA from experiment 4 were from the tagging vessel. However, because the tagged fish were released in the WA area, fishery 2 for analysis B is defined as the SA and WA areas combined. For both analyses, fishery 3 is the Japanese longline fishery with no geographical restrictions.

As mentioned earlier, the use of catch data to parameterize F involves an assumption that the population is in equilibrium for the duration of the tag-recovery period. This is not an unreasonable assumption for the juvenile population available to the surface

Table 4

Numbers of tag returns from experiment 2 and experiment 3 by period at liberty and related catch statistics used in analysis A of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963–70 for NSW and 1964–71 for SA. The Japanese (fishery 3) catch used is the 1964–85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia.

Time at liberty (yr)	Experiment 2 releases (NSW)			Experiment 3 releases (SA)			Catches ($t \times 10^3$)		
	Returns from			Returns from					
	NSW	SA	Japan	NSW	SA	Japan	NSW	SA	Japan
0–1	3144	55	4	159	842	14	3.445	3.968	45.216
1–2	854	24	12	37	77	24	3.748	3.825	45.216
2–3	64	8	17	7	3	28	4.232	4.089	45.216
3–4	5	0	4	0	0	23	4.177	4.213	45.216
4–5	0	0	2	0	0	23	4.569	4.395	45.216
5–6	2	0	0	0	0	12	4.418	4.896	45.216
6–7	0	0	3	0	0	9	3.815	5.588	45.216
7–8	0	0	2	0	0	3	3.681	5.815	45.216
8–9	0	0	1	0	0	8	3.772	6.005	45.216
9–10	0	0	1	0	0	3	3.594	6.315	45.216
10–11	0	0	2	0	0	1	3.256	6.695	45.216
11–12	0	0	0	0	0	2	3.438	7.415	45.216
12–13	0	0	0	0	0	0	2.984	8.539	45.216
13–14	0	0	0	0	0	0	2.788	8.974	45.216
14–15	0	0	0	0	0	0	2.764	9.284	45.216
15–16	0	0	0	0	0	0	2.163	10.178	45.216
16–17	0	0	1	0	0	1	1.626	10.856	45.216

Table 5

Numbers of tag returns from experiment 2 and experiment 4 by period at liberty and related catch statistics used in analysis B of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963–70 for NSW and 1964–71 for SA. The Japanese (fishery 3) catch used is the 1964–85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Time at liberty (yr)	Experiment 2 releases (NSW)			Experiment 4 releases (WA)			Catches ($t \times 10^3$)		
	Returns from			Returns from					
	NSW	SA/WA	Japan	NSW	SA/WA	Japan	NSW	SA/WA	Japan
0–1	3144	55	4	37	220	6	3.445	4.094	45.216
1–2	854	24	12	109	75	3	3.748	4.026	45.216
2–3	64	8	17	12	11	28	4.232	4.385	45.216
3–4	5	0	4	0	1	10	4.177	4.547	45.216
4–5	0	0	2	0	0	21	4.569	4.763	45.216
5–6	2	0	0	1	0	14	4.418	5.407	45.216
6–7	0	0	3	0	0	5	3.815	6.148	45.216
7–8	0	0	2	0	0	0	3.681	6.443	45.216
8–9	0	0	1	0	0	4	3.772	6.775	45.216
9–10	0	0	1	0	0	1	3.594	7.299	45.216
10–11	0	0	2	0	0	0	3.256	7.879	45.216
11–12	0	0	0	0	0	1	3.438	8.914	45.216
12–13	0	0	0	0	0	0	2.984	10.481	45.216
13–14	0	0	0	0	0	2	2.788	11.768	45.216
14–15	0	0	0	0	0	0	2.764	12.283	45.216
15–16	0	0	0	0	0	1	2.163	13.334	45.216
16–17	0	0	1	0	0	0	1.626	13.925	45.216
17–18	0	0	0	0	0	1	1.175	13.353	45.216

Table 6

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.7135	0.4354	0.6336	0.5673 E-1	0.5295	0.1105
M_2	0.1490 E+1	0.2555 E+1	0.1449 E+1	0.3114	0.1391 E+1	0.6542
M_3	0.2044	0.1264	0.2019	0.2636 E-1	0.1975	0.4307 E-1
q_1	0.2046	0.4249 E-2	0.2267	0.4705 E-2	0.2544	0.5276 E-2
q_2	0.8595 E-1	0.4330 E-2	0.9512 E-1	0.4806 E-2	0.1072	0.5397 E-2
q_3	0.6147 E-3	0.2762 E-2	0.6912 E-3	0.4003 E-3	0.7526 E-3	0.8415 E-3
T_{12}	0.1176	0.1330 E-1	0.1182	0.1347 E-1	0.1169	0.1322 E-1
T_{13}	0.9667 E-1	0.4348	0.9452 E-1	0.5432 E-1	0.9758 E-1	0.1092
T_{21}	0.1750	0.1435 E-1	0.1751	0.1437 E-1	0.1750	0.1437 E-1
T_{23}	0.5691	0.2553 E+1	0.5637	0.3283	0.5784	0.6462
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.3582	0.9196 E-1	0.2232	0.1346	0.8865 E-2	0.9048 E-1
M_2	0.1090 E+1	0.5488	0.1213 E+1	0.7968	0.1239 E+1	0.5315
M_3	0.2057	0.2837 E-1	0.1890	0.6001 E-1	0.1660	0.7660 E-1
q_1	0.2900	0.6015 E-2	0.3367	0.6969 E-2	0.4014	0.8306 E-2
q_2	0.1224	0.6177 E-2	0.1431	0.7218 E-2	0.1715	0.8655 E-2
q_3	0.6118 E-3	0.3980 E-3	0.9476 E-3	0.1225 E-2	0.1476 E-2	0.1649 E-2
T_{12}	0.1172	0.1326 E-1	0.1155	0.1312 E-1	0.1151	0.1301 E-1
T_{13}	0.1382	0.9035 E-1	0.1026	0.1339	0.7884 E-1	0.8817 E-1
T_{21}	0.1754	0.1440 E-1	0.1760	0.1441 E-1	0.1764	0.1443 E-1
T_{23}	0.8203	0.5449	0.6121	0.7933	0.4735	0.5314

fisheries as long as recruitment was reasonably constant during this period. The stability of the surface catches during the 1960s and early 1970s and cohort analysis (Hampton 1989) would suggest that this was the case. Although the adult population declined during several periods since exploitation began, Japanese catch was fairly constant during these tagging experiments, and parental biomass also appeared to be relatively stable. Therefore, the use of catch data to parameterize F should not cause major difficulties in this case.

In these experiments, tagged southern bluefin were released over a period of years; therefore, returns within a specific time-at-liberty category cannot be related to a catch in any one year. In these cases, the catch (or effort) data used are normally averaged over time, assuming a constant F within each fishery (e.g., Kleiber et al. 1987). This was the approach taken for the Japanese fishery, where catch was in fact quite constant over most of the return period (mid-1960s to early 1980s). For the Australian surface fisheries, an 8-year moving average (equivalent to the total release period for experiments 2, 3, and 4) was used so that the gradual decline of the NSW fishery and gradual increase in the SA and WA fisheries (Hampton 1989) could be represented.

Analysis A The first fit to the data allowed M to vary among the three fisheries. The resulting estimates of the three natural mortality parameters, three catchability parameters and four movement parameters and their standard errors, for reporting rates between 1.0 and 0.5, are presented in Table 6. There is no *a priori* reason why reporting rate should be the same for the three fisheries. In the absence of any information on the actual reporting rates, they have been assumed here, for simplicity, to be the same for the three fisheries.

For a reporting rate of 1.0, the estimates of M for the three fisheries are 0.71/year, 1.5/year, and 0.20/year, respectively. M_2 and M_3 decrease slightly as reporting rate decreases; however, M_1 decreases substantially with decreasing reporting rate. This is because the tag recapture rate in NSW is very high even if a reporting rate of 1.0 is assumed; therefore, even relatively small reductions in reporting rate from 1.0 require substantial compensatory changes in M_1.

Catchability in the NSW fishery is very high and suggests a fishing mortality rate of approximately 0.8/year, reflecting the high recapture rate there (33% of experiment 2 releases recaptured within 1 year and 42% recaptured within 2 years). Catchability is substantially lower in the SA and Japanese fisheries, suggesting rates of fishing mortality of approximately 0.35/year and 0.03/year, respectively. The catchability coefficients increase steadily with decreasing reporting rates, approximately doubling with a reduction in assumed reporting rate from 1.0 to 0.5. Rates of movement are slightly higher in the SA→NSW direction (0.17/year) than in the NSW→SA direction (0.12/year). Apparent movement into the Japanese fishery is substantially higher from the SA fishery (0.57/year) than from the NSW fishery (0.10/ year). The movement parameters are relatively unaffected by changing the assumed reporting rate within the range 1.0–0.5.

Table 7

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 6) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.99	1.00								
M_3	−0.98	−0.99	1.00							
q_1	0.01	−0.01	−0.01	1.00						
q_2	0.03	0.04	−0.03	−0.04	1.00					
q_3	0.99	0.99	−0.98	−0.01	0.02	1.00				
T_{12}	−0.06	−0.04	0.04	−0.09	−0.15	−0.04	1.00			
T_{21}	0.00	0.01	−0.01	−0.10	0.37	0.00	0.04	1.00		
T_{13}	−0.99	−0.99	0.98	0.01	−0.02	−0.99	−0.04	−0.00	1.00	
T_{23}	−0.99	−0.99	0.98	0.01	−0.02	−0.99	−0.04	0.00	0.99	1.00

The standard errors of the parameters are large, particularly for M_1, M_2, T_{13}, and T_{23}. The correlation matrix for the parameters (Table 7) indicates several cases of extreme confounding of estimates. The Ms are very highly correlated with one another and individually with q_3, T_{13}, and T_{23}. The latter three parameters are also very highly correlated with one another. These high correlations and standard errors suggest that the model is overdetermined (too many parameters).

Table 8

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M	0.2299	0.2326 E−1	0.2288	0.2285 E−1	0.2278	0.2224 E−1
q_1	0.2042	0.4244 E−2	0.2263	0.4697 E−2	0.2543	0.5278 E−2
q_2	0.8616 E−1	0.4341 E−1	0.9560 E−1	0.4820 E−2	0.1075	0.5416 E−2
q_3	0.1614 E−3	0.1981 E−4	0.1912 E−3	0.2349 E−4	0.2363 E−3	0.2917 E−4
T_{12}	0.1230	0.1393 E−1	0.1215	0.1372 E−1	0.1204	0.1355 E−1
T_{13}	0.5705	0.3142 E−1	0.4906	0.3050 E−1	0.3922	0.2923 E−1
T_{21}	0.1749	0.1433 E−1	0.1748	0.1434 E−1	0.1748	0.1432 E−1
T_{23}	0.1848 E+1	0.9067 E−1	0.1805 E+1	0.8919 E−1	0.1756 E+1	0.8755 E−1
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.2184	0.2061 E−1	0.1871	0.1717 E−1	0.1188	0.1360 E−1
q_1	0.2898	0.6007 E−2	0.3345	0.6881 E−2	0.3842	0.7657 E−2
q_2	0.1226	0.6181 E−2	0.1440	0.7239 E−2	0.1757	0.8793 E−2
q_3	0.2961 E−3	0.3617 E−4	0.3572 E−3	0.4162 E−4	0.3685 E−3	0.4209 E−4
T_{12}	0.1163	0.1295 E−1	0.1065	0.1164 E−1	0.8711 E−1	0.1536 E−1
T_{13}	0.2795	0.2638 E−1	0.1662	0.2031 E−1	0.8650 E−1	0.1259 E−1
T_{21}	0.1758	0.1440 E−1	0.1787	0.1458 E−1	0.1895	0.1536 E−1
T_{23}	0.1691 E+1	0.8503 E−1	0.1625 E+1	0.8109 E−1	0.1548 E+1	0.7539 E−1

Table 9

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 8) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M	1.00							
q_1	−0.02	1.00						
q_2	−0.04	−0.04	1.00					
q_3	0.81	−0.03	−0.06	1.00				
T_{12}	0.01	0.09	−0.16	0.05	1.00			
T_{21}	−0.02	−0.10	0.37	−0.02	−0.04	1.00		
T_{13}	−0.76	0.24	0.07	−0.65	−0.31	−0.05	1.00	
T_{23}	−0.30	−0.03	0.68	−0.26	0.06	0.39	0.17	1.00

Consequently, in the second fit to the data, M was assumed to be equal for the three fisheries (constrained M), thus reducing the number of parameters from ten to eight. A likelihood ratio test (Kendall and Stuart 1979) was conducted with the constrained-M fit defined as the null hypothesis and the unconstrained-M fit as the alternative hypothesis (assuming $R = 1.0$). The test indicated that the unconstrained-M fit was significantly better than the constrained-M fit ($P<0.01$). However, the constrained-M fit resulted in much smaller standard errors for the critical parameters (Table 8); q_3 has a coefficient of variation (CV) of 15%, with all other parameters having CVs of less than 10%. The correlation among the parameters is also much more acceptable (Table 9), although M is still correlated to a degree with q_3 and T_{13}, as are the qs with their respective incoming and outgoing movement parameters.

There are substantial changes in some of the parameter estimates obtained from the constrained-M fit. The overall estimate of M is 0.23/year, which is similar to the estimate of M_3 obtained from the unconstrained-M fit, but is much smaller than the M_1 and M_2 estimates. There is little change in q_1, q_2, T_{12}, or T_{21}; however, T_{13} and T_{23} are much larger in the constrained-M fit. These higher values compensate for the reduced M_1 and M_2 estimates (now assumed equal to M_3) in order to maintain the observed high rate of attrition of tagged fish in the NSW and SA fisheries. With the higher movement rates into the Japanese fishery, q_3 is smaller in the constrained-M fit so that the observed rate of return of tags from that fishery is still well described by the model. The estimate of M is insensitive to reductions in reporting rate to about 0.7, while the other parameter estimates behave similarly to those of the unconstrained-M fit.

Plots of observed numbers of returns and the numbers expected on the basis of the constrained-M fit for each of the release-recapture categories do not reveal any glaring deficiencies in the model (Fig. 2). Plotting expected numbers of returns using the unconstrained-M fit produced an essentially identical result.

Analysis B The results of the unconstrained-M fits to the results of experiments 2 and 4 are given in Table 10. The estimate of M_1 is substantially smaller (0.28/year) than that obtained from analysis A. To maintain the observed rate of attrition of tagged fish in the NSW

Table 10

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 5). All mortality and movement parameters are in units per year. Estimates were not available for reporting rates less than 0.8 because of a boundary condition on the M_1 estimate.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.2810	0.2446	0.1612	0.5384	0.3555 E−1	0.6471 E−1
M_2	0.1158 E+1	0.3541	0.1207 E+1	0.7392	0.1170 E+1	0.8124 E−1
M_3	0.1909	0.5157 E−1	0.2064	0.9149 E−1	0.2043	0.2620 E−1
q_1	0.2032	0.4287 E−2	0.2253	0.4768 E−2	0.2526	0.5369 E−2
q_2	0.9334 E−2	0.6819 E−3	0.1020 E−1	0.7734 E−3	0.1146 E−1	0.8439 E−3
q_3	0.4623 E−3	0.9814 E−3	0.4932 E−3	0.2231 E−2	0.4590 E−3	0.1241 E−3
T_{12}	0.5384	0.6562 E−1	0.5652	0.6965 E−1	0.5655	0.7271 E−1
T_{13}	0.1094	0.2329	0.1211	0.5424	0.1447	0.3296 E−1
T_{21}	0.4508 E−1	0.4324 E−2	0.4364 E−1	0.4265 E−2	0.4354 E−1	0.4232 E−2
T_{23}	0.1636	0.3466	0.1614	0.7162	0.1913	0.4084 E−1

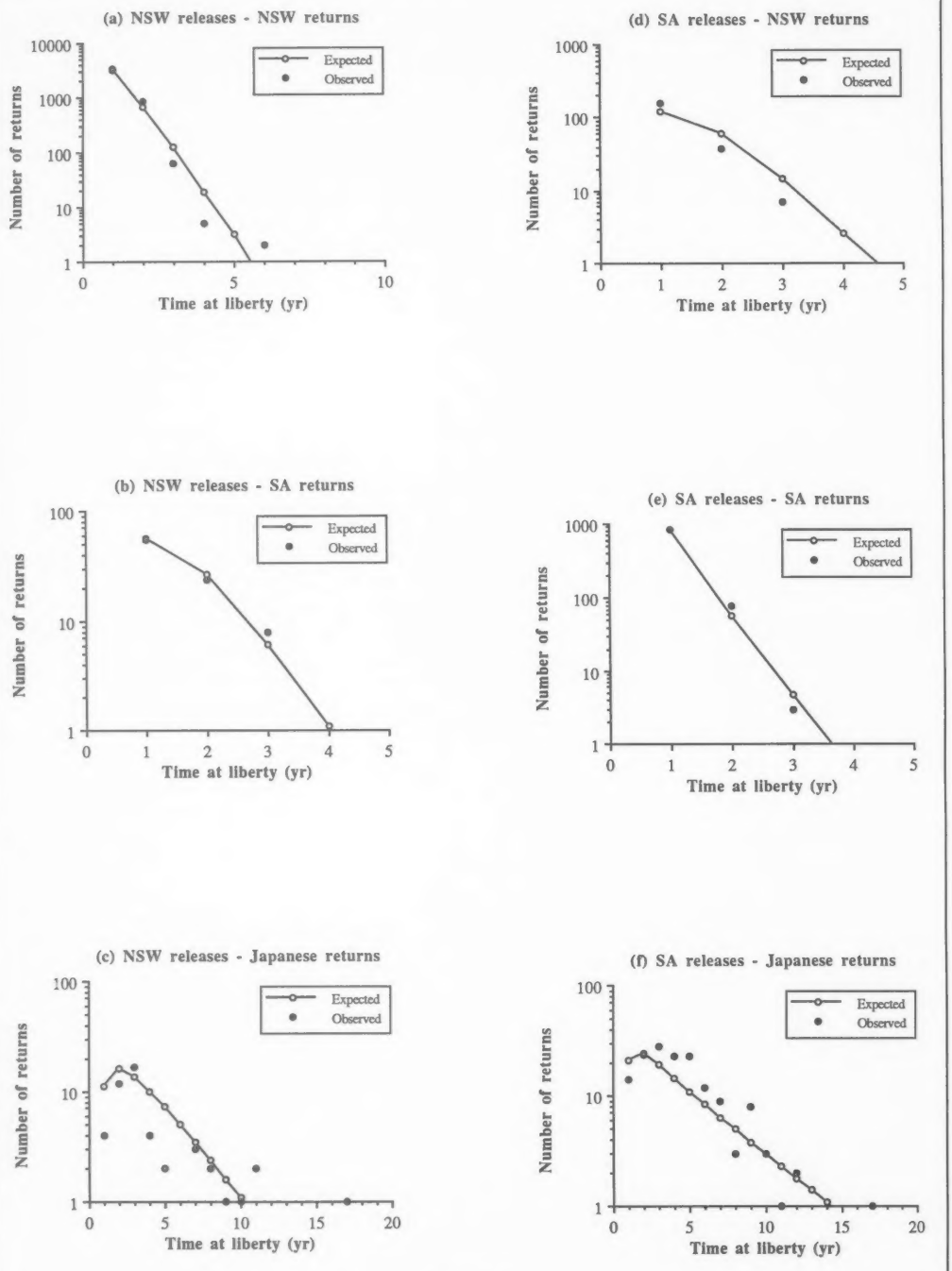
(a) NSW releases - NSW returns
Number of returns
Time at liberty (yr)
Expected
Observed
(d) SA releases - NSW returns
(b) NSW releases - SA returns
(e) SA releases - SA returns
(c) NSW releases - Japanese returns
(f) SA releases - Japanese returns

Figure 2

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis A. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 11

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 10) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.94	1.00								
M_3	−0.85	−0.87	1.00							
q_1	−0.01	−0.02	0.01	1.00						
q_2	0.10	0.14	−0.07	−0.07	1.00					
q_3	0.97	0.98	−0.86	−0.01	0.03	1.00				
T_{12}	−0.31	−0.05	0.07	0.13	−0.29	−0.07	1.00			
T_{21}	0.00	0.01	−0.03	−0.08	0.35	0.00	0.03	1.00		
T_{13}	−0.97	−0.98	0.87	0.01	−0.03	−0.99	0.06	−0.00	1.00	
T_{23}	−0.96	−0.98	0.88	0.01	−0.02	−0.99	0.07	0.01	0.99	1.00

fishery, a compensatory increase in T_{12} is observed. The estimate of M_2 is again relatively high (1.16/year) while the estimate of M_3 compares closely with that obtained from the unconstrained-M fit in analysis A. Recall that releases into fishery 2 (SA/WA) for analysis B were made some distance away from the commercial fishery operating at the time. This could explain the much lower estimate of q_2, and as a result, fishing mortality (~0.04/year). Similarly, the smaller estimates of movement from WA/SA into the NSW and Japanese fisheries is likely to be due to the fish being released further away from those fisheries.

The standard errors of the estimates that were obtained for the unconstrained-M fit are somewhat less than the equivalent values for analysis A, but are nonetheless far too high for the estimates to be considered reliable. The correlation matrix (Table 11) reveals a similar pattern of correlation among the parameters as was observed for analysis A.

It was not possible to obtain estimates of standard errors for reporting rates less than 0.8 because of a boundary condition with respect to the M_1 estimate, which approached zero for low reporting rates (the Hessian matrix could not be inverted because it was not positive definite). This also indicates that the parameter estimates obtained from this data set for reporting rates less than 0.8 are not the maximum likelihood estimates and therefore cannot be considered reliable.

A constrained-M fit resulted in much smaller standard errors, changes in parameter estimates consistent with analysis A (Table 12) and much lower correlation among parameters (Table 13). A likelihood ratio test (assuming $R = 1.0$) again indicated that the unconstrained-M fit is significantly better than the constrained-M fit ($P < 0.01$). However acceptance of the more complex model cannot be justified in view of the large standard errors and correlations among the parameter estimates. Plots of observed and expected numbers of returns (Fig. 3) indicate a good fit of the constrained-M model to the data.

Simulation results

Simulated data sets were analysed in order to test the performance of the HSH and SE models. The simulations were designed to produce data sets identical in their characteristics to experiment 2 and 3 (analysis A), with the exception that tag shedding and non-reporting were not considered. Two sets of simulations were performed: type 1 simulations used the results of the analysis A unconstrained-M fit as input parameters; type 2 simulations used the results of the analysis A constrained-M fit as input parameters. Thirty data sets were produced for each simulation. Type 1 simulated data were analysed by the SE model using both unconstrained-M and constrained-M fits. Type 2 simulated data were analysed using the SE model constrained-M fits and the HSH model in order to provide a basic comparison between the two models.

Parameter estimate means and their standard deviations for type 1 simulations are given in Table 14 for the unconstrained-M fits and Table 15 for the constrained-M fits. These results indicate that (i) the unconstrained-M fit provides unbiased estimates of all parameters, and (ii) the constrained-M fit to simulated data behaves in an identical fashion to similar fits to real data in terms of the changes in the estimates of q_3, T_{13}, and T_{23}. Moreover, the accurate recovery of parameters input to the simulation model demonstrates the soundness of the SE method as applied to southern bluefin tuna tagging data.

Table 16 provides a direct comparison of parameter estimates obtained by fitting the HSH and SE models to type 2 simulated data. The results indicate that the HSH model considerably overestimates M. The mean estimates from simulated experiments 2 and 3 and the mean estimate based on pooled data are almost identical (0.42–0.43/year) and are nearly double the value of M input to the simulation model. The SE model, on the other hand, is able to accurately retrieve the parameters input to the simulation model. This result casts considerable doubt on the estimates of M for southern bluefin tuna obtained using the HSH model.

The reason for the biased estimates of M obtained using the HSH model appears to lie in the very low

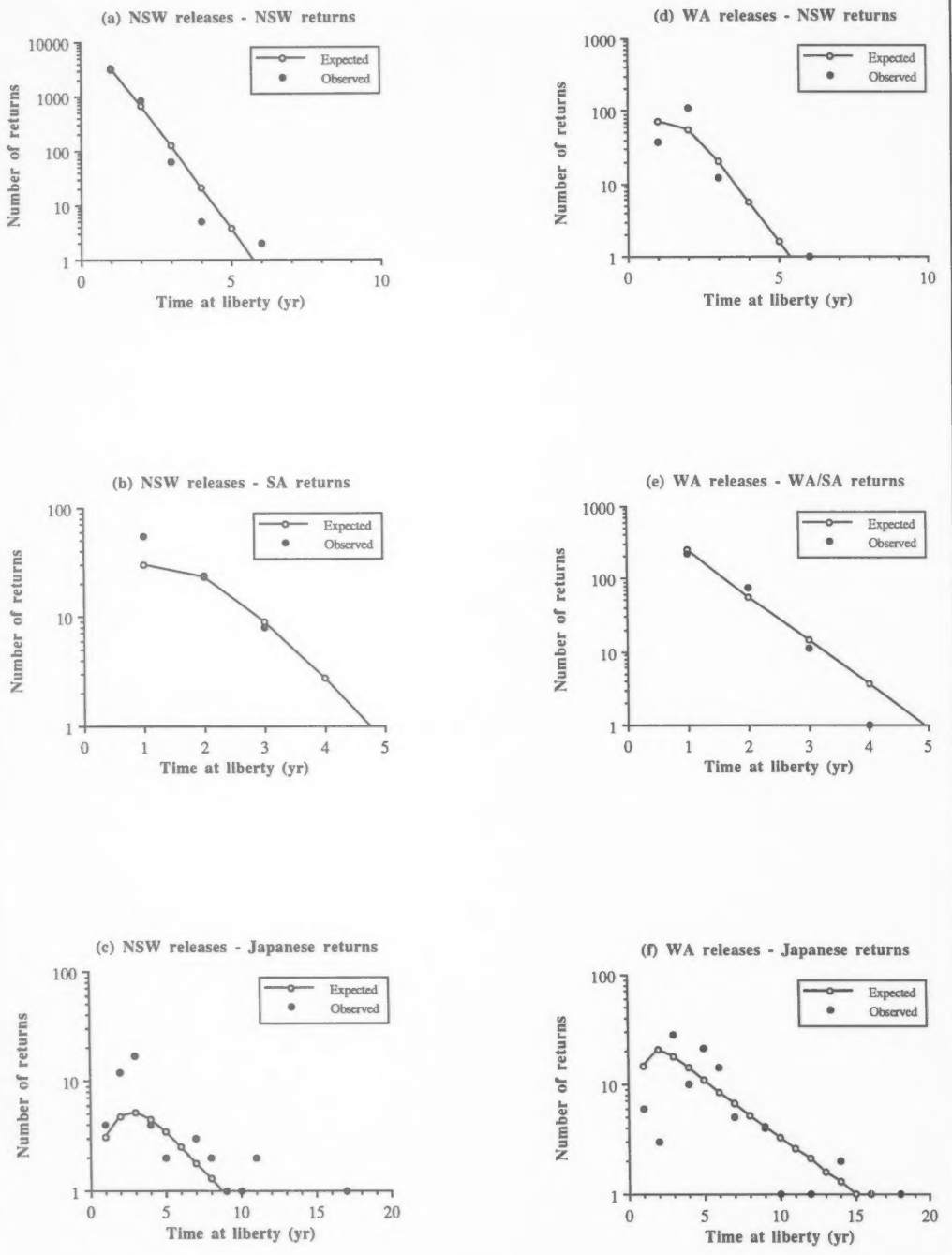
(a) NSW releases - NSW returns
Number of returns
Time at liberty (yr)
Expected
Observed
(d) WA releases - NSW returns
(b) NSW releases - SA returns
(e) WA releases - WA/SA returns
(c) NSW releases - Japanese returns
(f) WA releases - Japanese returns

Figure 3

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis B. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 12

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M	0.1997	0.2409 E−1	0.1902	0.2312 E−1	0.1775	0.2184 E−1
q_1	0.2034	0.4277 E−2	0.2253	0.4728 E−2	0.2524	0.5292 E−1
q_2	0.9575 E−2	0.6858 E−3	0.1076 E−1	0.7666 E−3	0.1221 E−1	0.8666 E−3
q_3	0.8078 E−4	0.1169 E−4	0.8863 E−4	0.1270 E−4	0.9765 E−4	0.1379 E−4
T_{12}	0.4123	0.4112 E−1	0.3837	0.3748 E−1	0.3475	0.3313 E−1
T_{13}	0.3163	0.4327 E−1	0.2748	0.3907 E−1	0.2249	0.3385 E−1
T_{21}	0.4429 E−1	0.4230 E−2	0.4470 E−1	0.4258 E−2	0.4489 E−1	0.4262 E−2
T_{23}	0.1082 E+1	0.7458 E−1	0.1087 E+1	0.7400 E−1	0.1083 E+1	0.7267 E−1
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.1575	0.2000 E−1	0.1215	0.1753 E−1	0.6137 E−1	0.1493 E−1
q_1	0.2857	0.5968 E−2	0.3272	0.6776 E−2	0.3746	0.7561 E−2
q_2	0.1422 E−1	0.1004 E−2	0.1701 E−1	0.1195 E−2	0.2106 E−1	0.1471 E−2
q_3	0.1055 E−3	0.1460 E−4	0.1073 E−3	0.1461 E−4	0.9352 E−4	0.1292 E−4
T_{12}	0.2994	0.2796 E−1	0.2389	0.2214 E−1	0.1694	0.1618 E−1
T_{13}	0.1713	0.2755 E−1	0.1175	0.2036 E−1	0.7254 E−1	0.1342 E−1
T_{21}	0.4534 E−1	0.4288 E−2	0.4643 E−1	0.4376 E−2	0.4936 E−1	0.4620 E−2
T_{23}	0.1091 E+1	0.7116 E−1	0.1109 E+1	0.6899 E−1	0.1151 E+1	0.6650 E−1

apparent fishing mortality inflicted upon the tagged population by the Japanese fishery. Recall that one of the assumptions of the HSH method is that fishing mortality is maintained on the tagged population until completion of the experiment. However, as F approaches zero for older age classes, overestimates of M result from this model. To confirm this, the type 2 simulations were rerun, with the only change being an increased input value of q_3 such that F for the Japanese fishery was increased to 0.2/year (the value derived from real data and previously used in the simulations involving the HSH method was 0.007/year). Under these conditions, the HSH model provided mean estimates of M of 0.24/year for the analysis of experiment 2, experiment 3, and the two experiments pooled. This agrees well with the value for M of 0.23/year input to the simulation model.

Table 13

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 12) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M	1.00							
q_1	0.02	1.00						
q_2	−0.07	−0.06	1.00					
q_3	0.81	0.02	−0.11	1.00				
T_{12}	−0.11	0.15	−0.21	−0.01	1.00			
T_{21}	−0.06	−0.09	0.36	−0.08	0.02	1.00		
T_{13}	−0.44	0.06	0.20	−0.43	−0.75	−0.05	1.00	
T_{23}	−0.45	−0.07	0.62	−0.41	0.07	0.48	0.16	1.00

Discussion

This paper represents the first specific attempt to estimate the southern bluefin tuna natural mortality rate from tagging data. The simulation results confirm that the method of Hearn et al. (1987) will overestimate M substantially when the apparent fishing mortality inflicted on the tagged population in the latter part of the experiment is very low. Also, the sensitivity of the M estimates to the tag-shedding model adopted makes interpretation of the results difficult, particularly as it was demonstrated by Hampton and Kirkwood (1990) that long-term shedding rates are very uncertain.

Table 14

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (unconstrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SD
M_1	0.71	0.69	0.016
M_2	1.49	1.55	0.087
M_3	0.20	0.20	0.018
q_1	0.20	0.21	0.0047
q_2	0.086	0.086	0.0040
q_3	0.00061	0.00067	0.000085
T_{12}	0.012	0.12	0.0099
T_{21}	0.017	0.18	0.014
T_{13}	0.097	0.11	0.011
T_{23}	0.57	0.53	0.067

Table 15

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SE
M_1	0.71		
M_2	1.49	0.23	0.016
M_3	0.20		
q_1	0.20	0.20	0.0044
q_2	0.086	0.087	0.0037
q_3	0.00061	0.00017	0.000018
T_{12}	0.012	0.12	0.015
T_{21}	0.017	0.17	0.014
T_{13}	0.097	0.51	0.029
T_{23}	0.57	1.86	0.088

Table 16

A comparison of mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the HSH and SE models (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SD
HSH model			
M (experiment 2)	0.23	0.42	0.023
M (experiment 3)	0.23	0.43	0.031
M (pooled data)	0.23	0.43	0.015
SE model			
M	0.23	0.23	0.016
q_1	0.20	0.20	0.0045
q_2	0.086	0.085	0.0043
q_3	0.00016	0.00016	0.000017
T_{12}	0.12	0.12	0.014
T_{21}	0.17	0.17	0.015
T_{13}	0.57	0.58	0.027
T_{23}	1.85	1.80	0.066

The development of a population dynamics model for tagged southern bluefin that incorporates movement between the NSW and SA/WA fisheries and offshore movement into the Japanese longline fishery, as well as natural mortality and fishery-specific catchability, appears to overcome these difficulties. Although the unconstrained-M version of the model could not provide useful parameter estimates because of high parameter correlation, accurate estimates were obtained by assuming that the natural mortality rate was the same in all fisheries, thus reducing the number of parameters to be estimated by two. For a large highly-mobile apex predator, this may not be an unreasonable assumption. However, this simplification of the model was not achieved without a small, though significant, loss in likelihood of the data.

The substantial differences in some of the parameter estimates produced by the unconstrained-M and constrained-M versions of the model simply mean that the observed data could have been produced in a number of alternative and similarly likely ways. It is unlikely that M could vary amongst the three fisheries as much as was suggested by the unconstrained-M estimates in analysis A. It is noteworthy, however, that the estimate of M_3 was similar for both analyses and also compared well with the constrained-M estimates.

Compliance with model assumptions is usually difficult to assess, and this case is no exception. Tag-shedding was incorporated into both models used; therefore, in theory, the tag-shedding assumption was satisfied. In practice, the estimated shedding rates are very uncertain, particularly for the older recaptures. It would be desirable in the future to develop a method whereby uncertainties in tag-shedding rates were reflected in the standard errors of the estimated mortality and movement parameters. This might be achieved by the simultaneous estimation of shedding, mortality, and movement rates from double-tagging data.

There are no data available on which the calculation of reporting rates could be based; all estimations were therefore carried out for a range of reporting rates. Fortunately, the M estimates were largely insensitive to assumed reporting rates greater than about 0.7 in the case of the constrained-M estimates. It is worth

noting that the high recovery rate of tags released in NSW would suggest a high reporting rate in that fishery at least.

The few data available suggest that mortality associated with tagging southern bluefin tuna is slight. Animals have been reported to survive in good condition for 80 hours in a live bait tank after having been tagged (Robins 1963). Furthermore, Hynd and Lucas (1974) considered that the behavior of the fish immediately following tagging was consistent with slight or no tagging mortality. Personal observations in the field also support this hypothesis. If tagging mortality occurred and was immediate or nearly so, its effect on the parameter estimates would be slight and identical to that of non-reporting. If there was significant, continuous tag-induced mortality (which is unlikely), M would tend to be overestimated by both methods used in this paper.

The assumption of constant M has not been tested in this paper, but the possibility that a model with age-dependent M might provide a better fit to the tagging data should not be ruled out. Generalization of the SE model in this regard would be possible and may yield useful results, although similar estimation problems to those of the unconstrained-M fits might occur.

The final assumption concerns equal vulnerability of the tagged and untagged populations and is possibly the most difficult with which to comply. Strict compliance would require that either the fishing effort is distributed randomly with respect to both the tagged and untagged populations, or that the tagged population is distributed randomly with respect to the untagged population. The first possibility is seldom seen in practice because fishermen tend to direct their effort in areas of high fish concentration. If these areas happen to coincide with the areas of tag release (as is often the case), the number of recaptures during the first period after release may be larger than expected. This would result in overestimates of M and other components of tag attrition using the SE method. Similarly, the second possibility is not usually feasible, as it would require tagged fish to be released over a wide area within a short space of time. However, for highly mobile tunas such as southern bluefin, mixing is likely to be rapid, thus lessening the problem to a large extent. In the case of the NSW fishery, many tagged fish were released prior to the fishing season, which would tend to enhance mixing. Division of the Australian fishery into two components also helps compliance with this assumption. From this point of view, even further stratification would have been desirable; however, this would greatly complicate the algebra and probably result in statistical problems with parameter estimation.

The fishing mortality inflicted on tagged southern bluefin by the Japanese fishery would appear to be slight (<0.06/year for assumed reporting rates >0.5) compared with values of 0.15–0.40/year obtained from cohort analysis (Hampton 1989). This discrepancy could result because southern bluefin migrating through Australian coastal waters are subsequently somewhat less available to the longline fishery than the population in general. Such differential availability to surface and longline fisheries has been noted for other tuna stocks, e.g., populations of yellowfin tuna in the Pacific (Lenarz and Zweifel 1979, Suzuki 1988) and Atlantic Oceans (Fonteneau 1986, Suzuki 1988). While not necessarily affecting the estimates of M, caution should be exercised in the interpretation of estimates of fishing mortality derived from these tagging experiments.

The results of estimations using the SE method were consistent in suggesting a value of M, in the Japanese fishery at least, of approximately 0.2/year. There was little information in the data regarding M in the Australian surface fisheries; however, a value similar to the above is not an unreasonable, if tentative, conclusion. Analysis of more recent tagging experiments may, in due course, help to resolve this question.

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Abstract.—The relationship between length and age of larval and juvenile shortbelly rockfish *Sebastes jordani*, determined from otolith microstructure, is complex. Models that assume size increases smoothly with age may not accurately describe growth in young-of-the-year rockfish. A segmented (piece-wise linear) regression model relating somatic and otolith size was used to back-calculate body length-at-age. The segments of this model coincide with different growth stanzas, which are separated by distinct life-history transitions. The composite function of this model, and a Gompertz curve relating otolith size and age, yielded a good fit to the back-calculated standard length-at-age data. Comparison of back-calculated with actual growth showed no evidence of size-selective mortality. The change in body length, as the number of otolith increments increased, was equal to the observed increase in length per day of a sequentially sampled cohort, validating the daily periodicity of the increments.

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Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*

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The abundance of young-of-the-year fish, and ultimately the number that reach maturity, varies greatly among years. Much of this variation is unrelated to the size of the spawning stock, and understanding its causes remains a central focus of fisheries research (e.g., Hjort 1914, Sissenwine 1984, Rothschild 1986, Hollowed et al. 1987, Sinclair 1988). Mortality agents, such as starvation (Hjort 1914, Lasker 1975 and 1978, Houde 1977 and 1978, Theilacker 1978 and 1981, Grover and Olla 1986) and predation (Hunter 1981, Hunter and Kimbrell 1980, Sissenwine 1984, Bailey and Houde 1989), can operate strongly during early stages, and it is clear that mortality rates of young fish are higher than those experienced by older fish (Miller et al. 1988). Interannual variation in year-class strength can depend upon the rate of growth early in life (Houde 1987 and 1989, Underwood and Fairweather 1989). Under most conditions, the more rapidly fish grow through early, high-risk stages, the fewer die; small changes in growth rate can thus lead to a major change in recruitment (Houde 1987). Knowledge of the processes affecting growth during the early life history may help predict the occurrence of strong year-classes.

Numerous mathematical models have been developed to describe the growth process, including the Gompertz, von Bertalanffy, logistic, and exponential functions (Ricker 1979). Although these models usually perform well on adult stages, they commonly falter in predicting growth during the first few weeks of life. For example, Phillips (1964) used a von Bertalanffy function to model growth of shortbelly rockfish *Sebastes jordani*. The model predicted growth of adults well, but its accuracy deteriorated for young-of-the-year fish. Because somatic growth during early stages can be affected by abrupt physiological changes (e.g., flexion, juvenile transformation, and settlement), models that predict growth during this period should reflect (or describe) this complexity (Ricker 1979).

Rockfish (*Sebastes* spp.) are an important component of the west coast groundfish fishery (PFMC 1989). Growth rates of young rockfish have been estimated from linear models relating length to age (Boehlert 1981, Boehlert and Yoklavich 1983, Penney and Evans 1985, Haldorson and Richards 1987, Woodbury and Ralston 1991). Because most of these studies examined a narrow range of ages, linear models fit the data adequately. Although Penney and Evans (1985) showed that a linear model explained much of the variation in length during larval and juvenile stages of redfish, back-calculated growth rates varied systematically with age; growth rate was relatively slow for young larvae, more rapid

for older larvae, and relatively slow again for juveniles. This suggests that it is possible to improve upon the linear model and provide a more accurate description of growth over the entire range of ages.

Since Pannella (1971) first discovered daily growth increments in otoliths, many researchers have used these microstructural features to study fish growth (see reviews in Campana and Neilson 1985, Jones 1986). By measuring the widths of daily increments within the otolith, and defining the relationship between standard length and otolith radius, one can back-calculate the somatic length of fish at any given age. This approach provides a powerful tool for estimating growth rates (e.g., Thorrold and Williams 1989). In this study, we used otolith microstructure to back-calculate the growth of larval and juvenile shortbelly rockfish *Sebastes jordani*. To do this we (1) determined when daily increments begin to form, (2) validated the daily periodicity of the increments, (3) developed a growth model for back-calculation, and (4) assessed the effects of size-selective mortality on back-calculated estimates of growth.

Table 1

Haul and collection data gathered during this study. On the first three cruises, larvae only were collected; on the May–June cruise, both larvae and juveniles were collected.

Dates (1989)	Research vessel	No. hauls	No. collected	No. aged
01 Feb.	RV *Ed Rickettes*	7	191	153
18 Feb.	RV *David Starr Jordan*	2	31	31
06 March	RV *Ed Ricketts*	5	27	10
14 May–13 June	RV *David Starr Jordan*	168	1262	55

Methods

Field collections

Larval and juvenile shortbelly rockfish were collected on four cruises between 1 February and 13 June 1989 (Table 1). All sampling was conducted along the central California coast from Cypress Pt. (Monterey Co.) to Pt. Reyes (Marin Co.). Larval samples were collected with oblique tows to maximum depths of 50–200 m, and were towed at depth for 30 seconds, at an approximate ship speed of one knot. Larval samples were collected with a 1 m plankton net (0.505 mm mesh) or, for the 18 February cruise, a 2×2 m Isaacs-Kidd trawl (2 mm mesh). For further information on larval hauls, see Appendix A. Larvae were sorted and placed in 80% ethanol. Juvenile samples were collected with a 26× 26 m midwater trawl (0.945 cm mesh codend liner), towed horizontally at depth for 15 minutes at a speed of approximately one knot. Sampling for the juvenile survey was at fixed stations spread throughout the study area, with target depths of 10, 30, and 100 m, but with most samples taken at the standard depth of 30 m. Juvenile rockfish were removed from hauls and immediately frozen. For further details on procedures for the juvenile survey, see Wyllie Echeverria et al. (1990).

To determine when daily otolith increments begin to form, gestating larvae (rockfish are viviparous livebearers) were collected and their otoliths examined. Adult female rockfish were collected during the May–June survey and from commercial fishermen at Fort Bragg, California in May. Preextrusion larvae were removed and placed in 80% alcohol for later examination.

Laboratory procedures

The stage of development of the gestating larvae was determined by morphology and pigmentation (Moser et al. 1977). Larvae from four females (two from the May–June cruise and two collected from commercial fishermen in May) were found to be in an advanced stage of development and were used for further analysis.

The standard length (SL) of all larvae and juveniles was measured to the nearest 0.1 mm. Ages were determined for juveniles spanning the entire size range collected and for all planktonic larvae. Sagittae were removed from each fish and affixed whole to slides with a drop of clear fingernail polish. Intact otoliths from larvae (<20 mm) had discernable growth increments with no further preparation. For fish with SL >20 mm, otoliths were sanded in the sagittal plane with 400-grit sandpaper until the nucleus became visible. Concentrated HCl was used to etch the otoliths until growth increments were easily discernable.

All otoliths were viewed at 600–1250× magnification with a compound microscope equipped with a video camera and monitor. Only fish with a dark check mark that clearly encircled the primordium were used in our analysis of growth (see also Penney and Evans 1985). Fish with this mark and no additional increments were given a nominal age of zero. Increments were counted from this mark to the most distal point along the postrostral growth axis. We used a digitizer to record the exact position of each increment; otolith radius (OR) was measured to the nearest 0.1 μm.

Validation

To validate that the increments were formed daily, we only considered samples collected during the May–June survey, because it was the only multiple-day cruise. From the data we identified a well-defined, temporally discrete cohort, and estimated the average change in length of individuals over the duration of the cruise. We compared this rate with the rate of change in length with nominal age from otoliths.

We identified a temporally discrete cohort as follows. Using the 55 aged fish (mainly juveniles) from the May–June cruise, and assuming that the number of increments approximated age in days after extrusion, we linearly regressed age on SL. From the resulting regression equation, we estimated the ages of all juveniles caught (all specimens were measured, but only a subsample of 55 fish from this cruise was aged). By subtracting estimates of age from known dates of capture (measured from the beginning of the year), we estimated the dates when the dark check mark formed for all fish sampled. A plot of frequency of occurrence against estimated dates of check mark deposition was used to identify the cohort. We stress that this procedure was used only to identify the cohort for further consideration. The rate of change in length-per-unit-time for fish sampled from the cohort was found by calculating the rate at which the lengths of captured individuals changed over the course of the 30 day cruise.

Data analysis

Initial exploratory model development involved fitting a number of equations (by least squares) to the data to characterize two functional relationships: OR = f(age) and SL = g(OR). For the former, we used not only the radius of the otolith at the time of collection (terminal OR), but also back-calculated radii measured at earlier ages. Due to the serial correlation present in these data (multiple observations of OR-at-age from the same fish), we used the grouped jackknife technique (Miller 1974) to estimate standard errors of the parameters. In contrast, we used only terminal values of OR and SL when fitting the latter relationship. Once known, the composition of these two functions $\{f^{o}g\}$ defined explicitly the dependence of SL on age, i.e., $\widehat{SL} = g(f(age))$. This procedure provided a better description of the age-length relationship than did the more usual approach of fitting a growth model to back-calculated SL-at-age data, even when complex formulations were tried (e.g., the two-stage Gompertz function suggested by Zweifel and Lasker 1976).

A single-stage Gompertz growth equation (Ricker 1979) provided a good description of otolith growth. The model has three parameters (OR_0, k, and g) and can be expressed as:

$$OR = OR_0 \cdot \exp\{k \cdot [1 - \exp(-g \cdot age)]\}.$$

Our data showed increasing variance in OR with increasing age, so the data and the equation were logarithmically transformed prior to fitting (Zweifel and Lasker 1976).

To regress SL on OR, we developed a model consisting of four linear segments, each describing a different growth stanza (see Appendix B for details). Before selecting this segmented model, we first considered, and then discarded due to lack of fit, a number of continuous models, including the simple two-parameter linear model, the Gompertz function, and three-parameter power and exponential models with separate Y-intercept terms.

Once we had established a relationship between SL and OR, we used this relationship to back-calculate SL at ages younger than the terminal age-at-capture. We used the "body-size proportional" method described by Francis (1990) in our back-calculations, in which the length at age i (some age younger than c, the age of collection) for fish j (SL_{ij}) is given by:

$$SL_{ij} = g(OR_{ij}) \cdot (SL_{cj}/g(OR_{cj})),$$

where, as above, $g(\cdot)$ is the regression equation we developed to predict expected SL from OR, and SL_{cj} is the measured length of fish j at the time of capture. Note that this method corrects for the deviation between the length predicted by the regression model and actual length at the time of capture. The well-known Fraser-Lee method, which also takes into account actual length of an individual at the time of capture, is inappropriate here because of the non-linear relationship between SL and OR (Campana 1990, Francis 1990). The fit of $\widehat{SL} = g(f(age))$ to the "observed" back-calculated estimates of SL_{ij} was then evaluated by examining a plot of the residuals ($SL_{ij} - \widehat{SL}$).

Results

We measured SL of 1511 larval and juvenile shortbelly rockfish. Ages were determined for 249 fish that ranged in size from 4.5 to 74.5 mm SL. Of these, 194 (4.5–15.2 mm SL) were from the three single-day cruises and 55 (14.6–74.5 mm) were from the May–June cruise (Table 1).

None of the gestating preextrusion larvae that we examined possessed the dark check mark that we used as the starting point for increment counts. Because of this, and the presence of increments in most of the

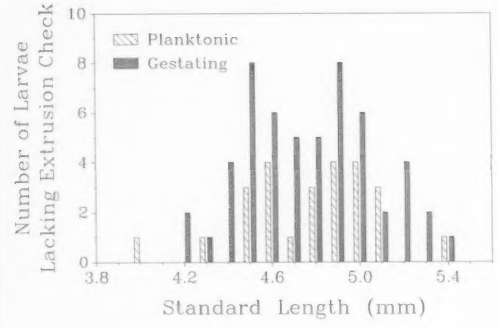

Figure 1
Size distributions of fully developed gestating (n 54) and planktonic (n 25) larvae of shortbelly rockfish lacking the extrusion check.

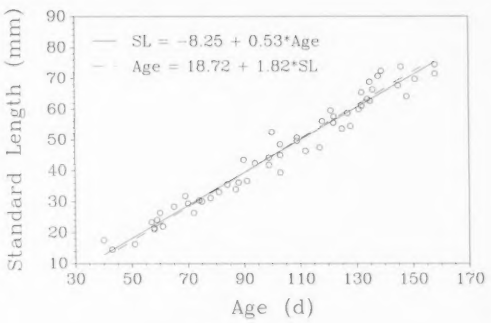

Figure 3
Least-squares regressions relating standard length and age for juvenile shortbelly rockfish collected during the May–June survey off central California, 1989.

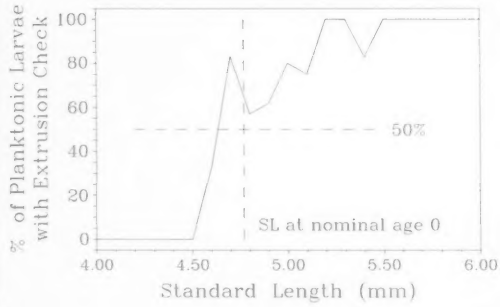

Figure 2
Change with length in the percentage of planktonic shortbelly rockfish larvae (n 25) exhibiting the extrusion check.

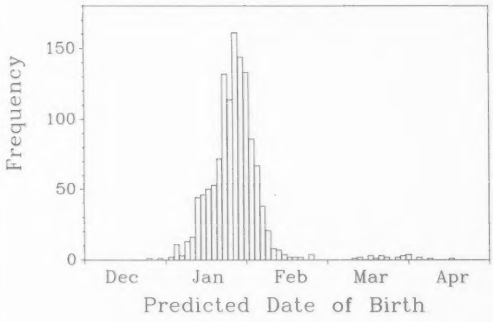

Figure 4
Frequency distribution of birthdates (date of extrusion check) for all shortbelly rockfish caught during the May-June survey off central California, 1989. Note the existence of a small but discrete second cohort spawned in March and April.

smallest planktonic larvae, we believe this mark was formed at, or shortly after, extrusion. The size distribution of the few planktonic larvae that lacked this feature (henceforth called the extrusion check) was similar to the size distribution of full-term, gestating larvae (Fig. 1). Thus, shortbelly rockfish do not appear to grow substantially from the time of extrusion to the time the extrusion check is formed. Likewise, all planktonic larvae greater than 5.5 mm in length had an extrusion check and more than 50% had the extrusion check, at a size of 4.7 mm (Fig. 2). The average size of the full-term gestating larvae we measured was 4.7 mm, and we take this as an estimate of the size-at-extrusion, which is independent of our growth models.

Validation

We compared how the mean SL of fish in a cohort changed over a 30-day period, with the growth rate estimated from a regression of SL on nominal age determined independently by examining otoliths. For the 55 fish we aged from the extended May–June cruise, a linear relationship existed between assumed daily age and SL, with a slope of 1.82 days/mm (SE 0.0484) and an r^2 of 0.963 (Fig. 3). The distribution of estimated birthdates for all juveniles caught during the cruise (N 1262) contained a small secondary mode (N 25) in March and April (Fig. 4). In our primary analysis, we considered only those fish with birthdates occurring in January or February (N 1237).

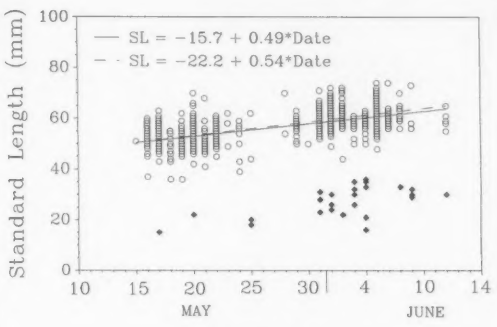

Figure 5

Regressions of standard length on calendar date of capture for all juvenile shortbelly rockfish taken during the May–June survey off central California, 1989 (solid line; r^2 0.265) and for the subset of juveniles that were extruded during the primary January–February spawn (open circles and dashed line; r^2 0.484). Diamonds represent the fish (n 25) spawned during March and April.

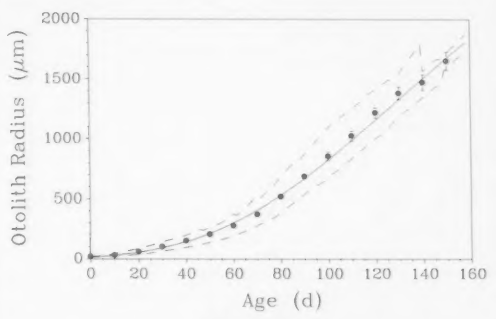

Figure 6

Predicted otolith radius as a function of age (solid line) from the Gompertz growth model (multiple observations from each specimen). Filled circles are means of the observed data at 10-day intervals, bracketed by ±2 standard errors. Note that standard errors for younger ages do not appear due to the resolution of the figure. Dashed lines enclose the range of data.

For the juveniles from the first cohort, the slope of the regression of SL on date of capture was 0.54 mm/day (SE 0.0158; Fig. 5). This compares with a slope of 0.53 mm/increment (SE 0.0140) obtained from a regression of length against the number of increments counted for the 55 aged fish (Fig. 3). Moreover, the slope of a regression of the predicted ages of the fish from the first cohort on their date of capture was 0.96 increments/day (SE 0.028). This rate is not significantly different ($P>0.05$) from the expected 1:1 correspondence between increments and days (t −1.43, df 1235).

Most of the fish from the second cohort (Fig. 4) were captured late in the May–June cruise, probably because selectivity of the net did not allow their capture at the beginning of the cruise when they were smaller. Because fish from the second cohort were smaller and were caught later in the cruise, excluding them improved the agreement between the observed rate of change in length over time and the growth rate estimated from daily otolith increments of aged fish (Fig. 3). We feel that the exclusion was warranted because of the clear separation between the cohorts (Fig. 4). In any case, relatively few fish (25 out of 1262) were excluded, and the effect on our estimated rate of change in length of the cohort was slight (~10%; Fig. 5).

Growth of the otolith

Otoliths of shortbelly rockfish grow at a generally increasing rate from birth to ~90 days in age (Fig. 6). Thereafter, there is substantially less curvature in the data. Results of fitting the Gompertz growth function to the data yielded estimates of $OR_0 = 16.00\,\mu m$ (SE 0.0374), k = 5.4223 [dimensionless] (SE 0.0235), and g = 0.01298/day (SE 0.000106), with an r^2 of 0.991. The curve (solid line in figure) fit the data well except for a minor lack of fit at about 70 days of age.

Standard length vs. otolith radius and back-calculation of length

The segmented linear model (after Bacon and Watts 1971) provided a good fit when SL was regressed on OR (Fig. 7, Table 2). There was no discernable pattern to the residuals, and the r^2 value was quite high (0.998). In addition, the model's estimate of body length at the mean otolith radius at the extrusion check (17 μm) was 4.9 mm SL; this approximated independent estimates of length-at-extrusion (5.4 mm [Moser et al. 1977], 4.0 mm [MacGregor 1986], and 4.7 mm SL [this study, Figs. 1, 2]). The intersections of the four linear segments relating SL to OR were at 38.7, 73.1, and 431.3 μm OR, and the corresponding lengths were 7.7, 8.4, and 29.9 mm SL, respectively.

Larvae were collected with two types (sizes) of nets. A possible source of bias in our results could arise from different selectivities of the nets (Somerton and Kobayashi 1989). For example, differential sampling by the nets may be responsible for the segmenting seen in Figure 7, although we do not believe this is the case. Even though, on average, the nets collected different sized fish, both types of nets captured fish in the range

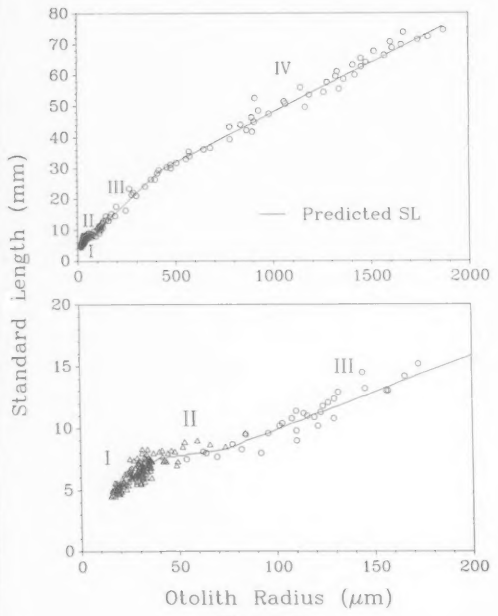

Figure 7

Plot of terminal standard length and otolith radius for all aged shortbelly rockfish (*N* 249). Shown is the predicted curve from the segmented model spanning the full range of data (upper panel), with Roman numerals for each of the four distinct growth stanzas. The lower panel enlarges the earliest growth stages (<200 μm OR). Circles are fish taken in Isaacs-Kidd trawls, and triangles are from plankton nets.

Table 2

Parameter estimates for the segmented regression model describing the relationship between standard length (mm) and otolith radius (OR, μm); Y-intercept (a), slopes for each segment (b_1–b_4), and intersection points of the segments (c_1–c_3) on the X (OR) axis. Note that, except for c_1–c_3, these are algebraic transformations of the actual parameters fitted by the regression procedure (see Appendix B). Estimates of length for a given OR based on the values given below ignore the smoothing described in Appendix B, but will be close approximations of the values that would be obtained using the original parameterization.

Transformed parameter	Estimate
a	2.92
b_1	0.1233
b_2	0.0219
b_3	0.0599
b_4	0.0327
c_1	38.72
c_2	73.10
c_3	431.31

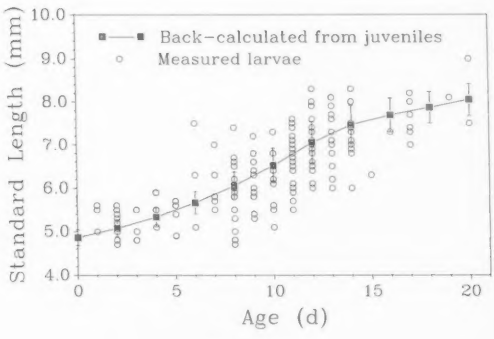

Figure 8

Scattergram of terminal standard length and age for larvae ≤20 days (open circles). Solid line depicts the back-calculated mean size-at-age (±1 SD) during the larval stage of juvenile fish (terminal age ≥60 days).

of 7.5–10.0 mm SL (lower panel of Figure 7). Within this range, the relationship of SL to OR did not differ significantly between the nets (t 0.50, df 4, $P>0.05$).

Standard length vs. age

Our back-calculation of standard length-at-age (SL_{ij}) is based on the implicit assumption that the mean back-calculated length at any particular age is similar to the mean length of fish actually captured at those earlier ages. Violation of this assumption is the so-called Rosa Lee's phenomenon (Ricker 1979), which can arise when mortality rates are size-selective and from a number of other causes, such as biased sampling. However, our data show that mean length-at-age during the first 20 days of life, back-calculated from juveniles at least 60 days old, passes through the observed values of SL and age at the time of capture for young larvae (Fig. 8). This result suggests that Rosa Lee's phenomenon is unlikely to distort our findings to any appreciable degree.

The predicted fit of the composite function [$\widehat{SL} = g(f(age))$] to the back-calculated size data was good (Fig. 9). Note that individual fish followed their own growth trajectories, producing serial correlation in the residuals. The slight lack of fit around age = 70 days (see Figure 6) is also seen more easily in this figure.

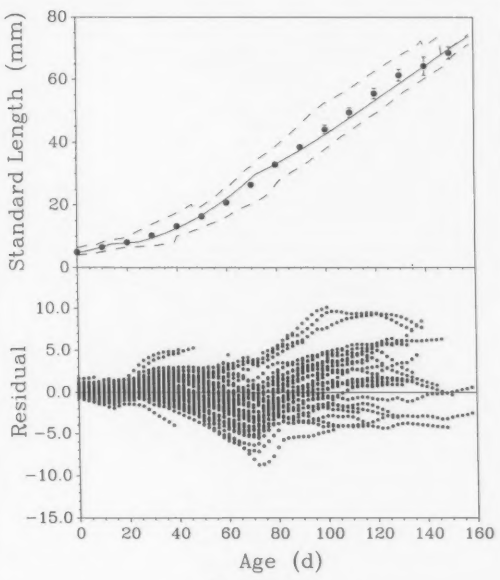

Figure 9

Relationship between back-calculated standard length and age for shortbelly rockfish. Solid line in the upper panel represents the composite function of relationships shown in Figures 6 and 7. Filled circles are means of the observed data at 10-day intervals, bracketed by ±2 standard errors. Dashed lines enclose the range of data. Residuals (observed–predicted) of the fit are shown below.

Discussion

Our goal was to develop a model that could be used to provide accurate estimates of back-calculated growth from the otolith microstructure of larval and juvenile shortbelly rockfish. A crucial assumption of the study was that the increments were formed daily. Many authors have stressed the importance of validating the daily periodicity of otolith growth increments (Jones 1986, Geffen 1987). Without validation, growth rates may be biased and their use in models of juvenile dynamics and recruitment could lead to serious errors. For validation purposes, we followed a cohort of fish through the May–June time period, measuring their progressive change in average length. We found that the rate of change in length of this cohort agreed with the estimated growth rate based on a regression of length against number of growth increments enumerated for aged fish. From this result, we conclude that the increments we counted were formed daily. It is noted, however, that the daily periodicity of these increments is validated only for the size ranges and dates observed during the extended May–June cruise, but we have no reason to assume that the increments are not daily at earlier stages of growth.

Other evidence exists that daily increments form in otoliths of *Sebastes* spp. Yoklavich and Boehlert (1987) demonstrated the daily periodicity of increment formation in otoliths of black rockfish *S. melanops* by marking the otoliths with oxytetracycline (OTC) and by autoradiography. Also, Laidig (unpubl. data) found no difference between increment counts and the number of days following a fluorescent OTC mark, verifying that the increments of brown rockfish *S. auriculatus* were interpreted correctly as daily.

Our segmented model of fish size versus otolith size, for use in back-calculating fish length, may describe significant events during the early life of *S. jordani*. The first major events following extrusion, in the early life of rockfish, are first feeding, flexion, and transformation from larva to juvenile. Moser et al. (1977) noted that shortbelly rockfish larvae undergo flexion at 8.0–10.0 mm SL. This range essentially corresponds to the size of fish in segment II. The slope of this segment was much reduced, suggesting that although fish length increases little during flexion, the otolith continues to grow. Likewise, Moser et al. (1977) found that juvenile transformation began after 27 mm SL, and we observed that the intersection of segments III and IV occurred at a length of about 30 mm SL. It is possible, of course, that the segments we have described are peculiar to the time and place that we collected the fish. For example, the slope of the fish size to otolith size relationship could have changed at specific points in time in response to altering oceanographic conditions (see also the discussion on "buffering" below). Before this type of alternative explanation can be discarded, similar SL–OR regressions need to be established in other years.

Relative to the entire organism, the sagittal otolith is a simple structure, especially during early life history. During the first 160 days of life, the sagitta develops from a spherical primordium into an oval-saucer shape. During this time a single Gompertz curve (Fig. 6) adequately described growth along one of its dimensions (i.e., the postrostral axis).

In contrast, the whole organism is morphologically and developmentally complex. Although a simple Gompertz curve, when fitted to back-calculated length (SL_{ij}) against age, resulted in a high r^2 value, an unacceptable pattern was evident in a plot of the residuals. Other authors also have found that smooth models (e.g., Gompertz and von Bertalanffy curves) did not accurately fit SL-at-age data in young-of-the-year fish (Uchiyama and Struhsaker 1981, Bailey 1982, Rosenberg and Laroche 1982, Campana 1984, Boehlert and Yoklavich 1985). Although these simplified models

often perform well on adult fish, they are sometimes unable to depict the complex growth processes characterizing the complete life history. In such cases, segmented models should be considered because they allow for life history changes and growth stanzas (Ricker 1979). For example, Watanabe et al. (1988) found that for Pacific saury *Cololabis saira*, two Gompertz curves produced a better fit to the relationship of length and the number of daily otolith increments than did a single Gompertz curve. Zweifel and Lasker (1976) showed that a two-stage Gompertz curve described the growth of anchovy *Engraulis mordax* larvae better than a simple single-stage Gompertz curve. These authors also noted that although other models had high coefficients of determination, they exhibited unacceptable predictions for small larvae. Likewise, Nishimura and Yamada (1988) found that three linear segments described the relationship between otolith length and total length for walleye pollock *Theragra chalcogramma*, and that the intersection points between segments represented changes from larval to juvenile growth and juvenile to adult growth.

Changes in growth stages or stanzas are characterized by a fundamental alteration or discontinuity in development, such as hatching, first feeding, maturation, or a change in habitat (Ricker 1979). Above we presented and reviewed some evidence for this idea from studies of fish. The concept is likely to have validity for many organisms. For example, allometric relationships for physiological rates in *Daphnia* are stage-dependent (McCauley et al. 1990).

Some authors (Reznick et al. 1989, Secor and Dean 1989) have shown that otolith growth rate is relatively insensitive to factors that cause more extensive variation in somatic growth rate (e.g., alterations in temperature and food ration). Under extreme conditions, however, daily increment deposition arrests or is otherwise seriously perturbed (Tanaka et al. 1981, Campana 1983, Neilson and Geen 1985; reviews in Campana and Neilson 1985 and Jones 1986). Nonetheless, in many instances the otolith can be considered a conservative growth structure that is buffered from environmental factors affecting somatic growth. The otolith continues to record significant events, such as transitions to other life stages, even when somatic growth is seriously impaired. Conversely, this buffering tends to obscure the otolithic record of somatic growth fluctuations arising from exogenous factors, e.g., temperature fluctuation, changes in prey density, and turbidity.

Insulation of the otolith to ambient conditions can lead to a somatic:otolith size ratio that is positively related to growth rate. Recently, Campana (1990) showed that this can lead to biased estimates of length-at-age and the appearance of Rosa Lee's phenomenon, when lengths are back-calculated by the Fraser-Lee method. He noted that this problem is unlikely to be significant when the intercept is well fixed by aging young larval fish, or through use of independent biological measurements. In our study, many of the aged fish were young larvae. In addition, the estimated length of a fish with an otolith radius equal to the mean radius at the extrusion check was in good agreement with the mean length of late-stage gestating pre-extrusion larvae. Lastly, we found no evidence that back-calculated lengths of fish captured as juveniles differed from directly measured lengths of fish captured as larvae.

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Appendix A

Detailed information on individual larval hauls.

Date	Research vessel	Gear type	Max. depth	Lat.	Long.	No. caught	No. aged
2/1	RV *Ed Ricketts*	Plankton net	150	36°48.2′	121°51.9′	22	15
2/1	"	"	150	36°48.1′	121°52.7′	42	27
2/1	"	"	100	36°47.8′	121°54.0′	27	5
2/1	"	"	100	36°47.8′	121°54.7′	48	34
2/1	"	"	200	36°47.9′	121°53.7′	32	18
2/1	"	"	80	36°48.4′	121°53.2′	36	33
2/1	"	"	100	36°48.3′	121°52.4′	13	4
2/18	RV *David Starr Jordan*	Isaacs-Kidd trawl	200	37°16.6′	122°49.1′	0	0
2/18	"	"	200	37°16.7′	122°49.0′	32	31
3/6	RV *Ed Ricketts*	Plankton net	100	36°48.2′	121°52.7′	2	1
3/6	"	"	120	36°47.8′	121°53.7′	5	4
3/6	"	"	140	36°47.2′	121°55.2′	6	6
3/6	"	"	130	36°46.4′	121°59.6′	4	4
3/6	"	"	60	36°47.2′	121°50.6′	12	8

Appendix B

Here we describe the regression model used to relate standard length to otolith radius, which consisted of a series of four linear segments, each describing a different growth stanza. We start with the following equation:

$$SL = \begin{cases} a + b_1 x \text{ for } x < c_1 \\ a + b_1 c_1 + b_2(x - c_1) \text{ for } c_1 \leq x < c_2 \\ a + b_1 c_1 + b_2(c_2 - c_1) + b_3(x - c_2) \text{ for } c_2 \leq x < c_3 \\ a + b_1 c_1 + b_2(c_2 - c_1) + b_3(c_3 - c_2) + b_4(x - c_3) \text{ for } c_3 \leq x \end{cases} \quad (1)$$

where a is the y-intercept of the first segment, x is the otolith radius, b_1, b_2, b_3, and b_4 are the slopes of the four segments, and c_1, c_2, and c_3 are the points on the x axis corresponding to the intersections. Because not all individuals would be expected to make the transition from one stanza to the next at identical sizes, it is reasonable to smooth the relationship at the segment intersections. We therefore applied the technique described by Bacon and Watts (1971) to smooth the transition between linear segments, assuming that most fish made the transition from one stanza to the next over a small size range. Specifically, we assumed that the probability that an individual fish made the transition from one stanza to the next was described by the logistic cumulative distribution function, $F(z) = 1/(1+\exp(-z))$, where $z = (x - c_i)/g$. Note that g is a constant chosen so that 95% of all transitions occur within $\pm 0.3\mu$m OR of each intersection. (We assumed this rapid rate of transition rather than evaluating the transition rate from the data because preliminary analyses, with g as an estimated parameter, indicated that the density of measurements on the x axis was not sufficient to yield unique solutions. Runs with different starting parameters did not converge to the same parameter estimates.) Following Bacon and Watts (1971), we rewrote the model as:

$$SL = e + d_1(x - c_1) + d_2(x - c_1)s_1 + d_3(x - c_2)s_2 + d_4(x - c_3)s_3 \quad (2)$$

where the terms relate to equation 1 as follows:

$$s_i = 2*(F((x - c_i)/g) - 1;\ i = 1,2,3;\ g = 0.1,$$

$$d_1 = (b_1 + b_4)/2,\ d_2 = (b_2 - b_1)/2,$$

$$d_3 = (b_3 - b_2)/2,$$

$$d_4 = (b_4 - b_3)/2, \text{ and}$$

$$e = a + ((b_1 + b_4)/2)c_1 - ((b_2 - b_1)/2)c_1 - ((b_3 - b_2)/2)c_2 - ((b_4 - b_3)/2)c_3.$$

Our estimates of the above parameters and their standard errors are in Appendix Table 1.

Appendix table 1

Parameter estimates for segmented SL vs. OR regression model, and their associated standard errors (SE).

Parameter	Estimate	SE
e	12.375	0.411
d_1	0.0780	0.0078
d_2	−0.0507	0.016
d_3	0.0190	0.014
d_4	−0.0136	0.00091
c_1	3.872	0.480
c_2	7.310	2.044
c_3	43.131	2.128

Abstract.– A new species of ghost shrimp *Lepidophthalmus sinuensis* is described from the Caribbean coast of Colombia, and general ecological observations are made on the conditions under which it was found. The new species can be distinguished from others in the genus by the presence of large subrectangular lateral projections on the frontal region of the carapace. The new species was discovered in ponds of a commercial penaeid shrimp farm where its burrow densities range up to 2093 burrow openings/m^2 in pond bottoms consisting of fine sand. It appears that, on at least a temporary basis, activities of *L. sinuensis* may negatively impact penaeid shrimp culture.

Lepidophthalmus sinuensis: A New Species of Ghost Shrimp (Decapoda: Thalassinidea: Callianassidae) of Importance to the Commercial Culture of Penaeid Shrimps on the Caribbean Coast of Colombia, with Observations on its Ecology

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During the first few months of 1990, penaeid shrimp production in several of the older ponds of a penaeid shrimp farm owned by the company Agrosoledad S.A. (located south of Cartagena, on the Caribbean coast of Colombia) began unexpectedly to decrease. Symptoms in the affected ponds during the grow-out cycles were: sustained low dissolved oxygen concentrations, an unusually high number of thalassinid burrows on the bottom, and small (unmarketable) shrimp in the harvest. About 50% of the ponds of the farm appeared to be affected. Other shrimp farms along this coast, however, were not affected. In July of 1990, biologists from the company, suspecting that the thalassinid might be the cause of the problem, sent specimens to one of us (RL) for identification. Our examination of the material revealed that the specimens represented a new species of the family Callianassidae. Subsequently, we traveled to the shrimp farm to obtain additional samples and make observations. Included herein is the description of this new species as well as some general ecological observations on the conditions under which it was found.

The discovery of this new callianassid is of significance to the rapidly growing industry of penaeid shrimp culture in Colombia. In 1990, the 1504 ha of ponds that were in production on the Caribbean coast alone produced a total harvest of 4314 metric tons of whole shrimp, valued at US$22.4 million. The shrimp produced is a mixture of *Penaeus vannamei* Boone, and *P. stylirostris* Stimpson. Although in Asian countries and western North America, thalassinids are known to cause damage to aquaculture operations, paddy fields, and engineering projects (e.g., Scharff and Tweedie 1942, Sankolli 1963, MacGinitie and MacGinitie 1968, ASEAN 1978), this is the first known case in the New World where a thalassinid has been proposed as potentially affecting penaeid shrimp mariculture.

The material of the new species has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), Museu de Zoologia da Universidade de São Paulo, Brazil

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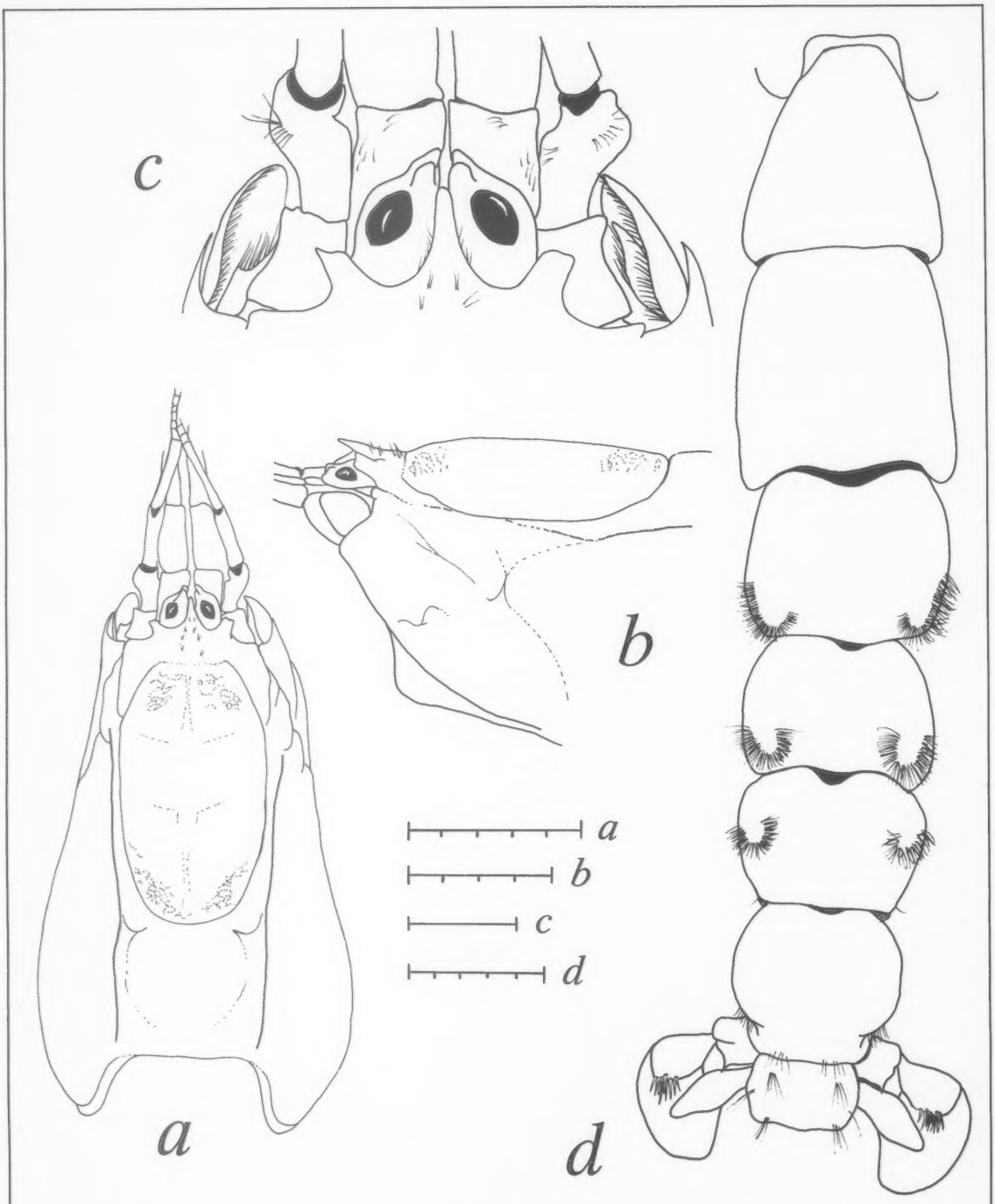

Figure 1

Lepidophthalmus sinuensis new species. (a) Carapace and cephalic appendages (dorsal view); (b) anterior portion of carapace and cephalic appendages (lateral view); (c) frontal region and cephalic appendages (dorsal view); (d) abdomen and tail fan (dorsal view). (a–c) Male CL 11.5 mm; (d) female CL 9.8 mm. Scales equal 5 mm (a, d), 4 mm (b), 1 mm (c).

(MZUSP), and in the zoological collections of the University of Southwestern Louisiana, Lafayette (USLZ). The abbreviation "CL" refers to carapace length measured along the dorsal midline from the level of the posterior orbital margin to the posterior end of the carapace. Two *in situ* burrow casts were made using epoxy resin (Araldit with hardener), following the method described by Dworschak (1983).

Lepidophthalmus sinuensis new species
Figures 1–4

Material examined

Agrosoledad S.A. shrimp farm, 3 mi inland from mouth of Rio Sinú, Departamento de Cordoba, Colombia (9°17′N, 75°50′W): 1 ♂, holotype (CL 11.8 mm), pond 5, 20 Aug. 1990, USNM 252399; 25 ♂ (CL 5.2–13.4 mm), 24 ♀ (CL 3.5–9.1 mm), pond 5, 20 Aug. 1990, USNM 252400, 252401, MZUSP 10751, USLZ 3027; 5 ♂ (CL 4.9–11.6 mm), 5 ♀ (1 ovig.) (CL 7.2–10.3 mm), pond 7, 20 Aug. 1990, USNM 252402. Bungalow beach near San Bernardo del Viento, Departamento de Córdoba, Colombia (9°17′N, 76°00′W): 1 ♂ (CL 11.0 mm), 5 ♀ (1 ovig.) (CL 8.3–11.8 mm), July 1990, coll. J. Araújo, USNM 252404, 252405; 3 ♂ (CL 10.5–13.8 mm), 7 ♀ (1 ovig.) (CL 8.6–13.2 mm), drainage canal, 20 Aug. 1990, USNM 252403.

Description

Frontal margin of carapace with blunt rostral spine and two fixed subrectangular lateral projections (Fig. 1c); rostral spine and lateral projections directed slightly upward; rostral spine reaching to about 2/3 length of eyestalks, lateral projections reaching to about midlength of rostrum. Anterior margin of carapace level between subrectangular lateral projections and margin of antennal peduncle, then curving forward to anterolateral angle of branchiostegite. Dorsal oval about 0.6 times length of carapace, smooth, weakly delimited anteriorly.

Eyestalks reaching to about 2/3 length of basal antennular segment, terminating distally in two subtriangular blunt protuberances (shorter dorsal, larger ventral). Cornea small, pigmented, centrally situated on the eyestalk. Antennular peduncle stouter than antennal peduncle, first (basal) segment shorter than second; third segment about 2.5 times as long as second; second and third segments with dense setation on ventral margin; flagellum with subequal rami. Antennal peduncle reaching to about midlength of ultimate antennular segment; flagellum about twice as long as antennular flagellum.

Mandible with several teeth on molar process, and long two-segmented palp. Maxillule with endopod curved distally. Maxilla, first and second maxillipeds as figured (Fig. 2c–e). Third maxilliped with slender, curved dactyl shorter and narrower than propodus; propodus about as long as wide, outer surface naked, inner surface with tuft of setae on posterior half; carpus with tuft of setae on inner surface near distal margin; with rudimentary exopod.

Branchial formula:

	maxillipeds			pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	—	—
Arthrobranchs	—	1*	2	2	2	2	2	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	1*	—	—	—	—	—

* rudimentary

Chelipeds strongly dissimilar, major cheliped on right or left side. Sexual dimorphism evident on major and minor chelipeds. Major cheliped of male (Fig. 3a) massive, reaching to about tip of antennal flagellum. Fingers leaving large gap proximally when closed. Dactyl longer than palm, smooth except for tufts of setae on dorsal margin and on basal outer surface of teeth; prehensile edge with 4–6 large, unequal, rounded teeth; inner face of dactyl with deep longitudinal groove. Fixed finger with strong tooth (pointing slightly outward and forward) near middle of prehensile edge and under second tooth of dactyl. Palm with scattered tufts of setae on outer face, row of tufts of setae on dorsal margin, and tufts of very long setae (reaching to about 2/3 length of dactyl) near dorsomesial distal angle; dorsal and ventral margin defined by keel-like ridge; outer face with several small tubercles bearing tufts of setae on sloping depression near base of fixed finger; inner face of palm (Fig. 3b) with tubercles bearing tufts of setae on ventromesial margin and on sloping depression near base of fixed finger. Carpus longer than palm, broader than long, dorsal and ventral margin defined by keel-like ridge, with small blunt tooth on dorsodistal and ventrodistal angle. Merus about as long as carpus, with row of three blunt spines on ventromesial distal margin. Ischium slender, slightly shorter than merus, armed with row of 14 small spines on ventrolateral margin.

Major cheliped of female strong but shorter, less high than in male. Fingers with tips strongly curved inward, crossing when closed; prehensile edge of dactyl and fixed finger straight or irregular (Fig. 3d, e), with small rounded teeth; fixed finger usually with strong, sharp tooth basally on outer face. Merus with ventromesial distal row of blunt to sharp spines, and usually with

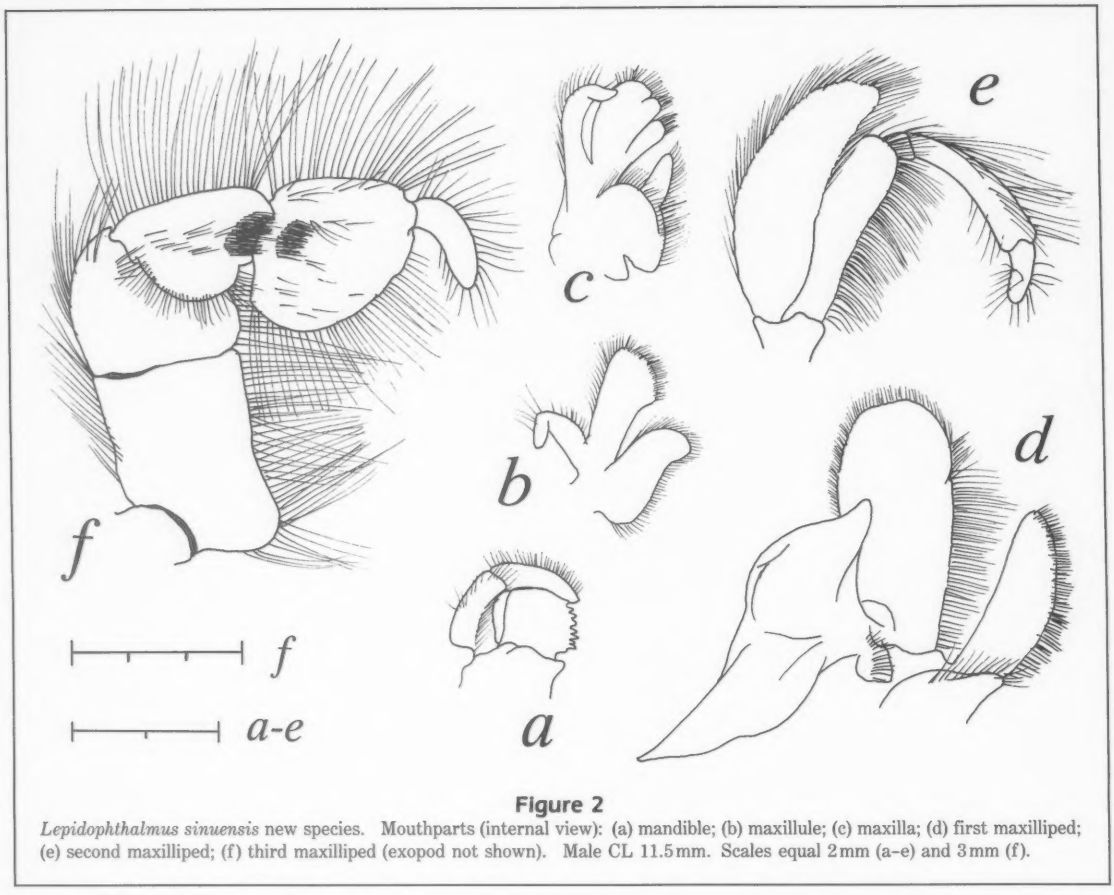

Figure 2

Lepidophthalmus sinuensis new species. Mouthparts (internal view): (a) mandible; (b) maxillule; (c) maxilla; (d) first maxilliped; (e) second maxilliped; (f) third maxilliped (exopod not shown). Male CL 11.5mm. Scales equal 2mm (a–e) and 3mm (f).

slender, curved spine on lateroproximal angle. Ischium with row of 16–17 small spines on ventrolateral margin.

Minor cheliped of male reaching to about level of bases of fingers of major cheliped. Fingers gaping when closed; prehensile edges of fingers formed by ridge of small rounded teeth. Dactyl with row of tufts of setae on dorsal and ventrolateral margin. Fixed finger with dense, brush-like setae basally on prehensile edge (Fig. 3c). Merus with slender curved spine on lateroproximal angle. Ischium with row of 18 small spines on ventrolateral margin.

Minor cheliped of female similar to that of male but somewhat slenderer, lacking brush-like setae on fixed finger.

Second pair of pereopods chelate, subequal; margins of chela and carpus setose; ventral margin of merus with row of evenly spaced long setae. Third pereopod with dactyl slightly longer than broad, subtriangular. Margins of dactyl and propodus with long setae. Propodus with ventral margin divided into three unequal lobes (medial one smallest); outer face covered with numerous tufts of short setae. Fourth pereopod subchelate; propodus and dactyl with setae, densely setose grooming apparatus on ventral margin of propodus. Fifth pereopod subchelate; propodus and dactyl with setae, densely setose grooming apparatus on suboval area covering most of inner face of propodus.

Abdominal somites smooth; dorsal surface naked except for line of dense setae forming sub-semioval near posterolateral angles of each somites 3 and 4 and on midline of somite 5, and line of short setae on posterolateral angle of somite 6 (Fig. 1d). Male first pleopod uniramous, two-segmented (Fig. 4c); distal segment with long setae, terminating in subtriangular tip with small lobe at base on anterior margin; basal segment two times (or more) as long as distal segment. Male second pleopod biramous, with appendix interna on endopod (Fig. 4d). Female first pleopod uniramous,

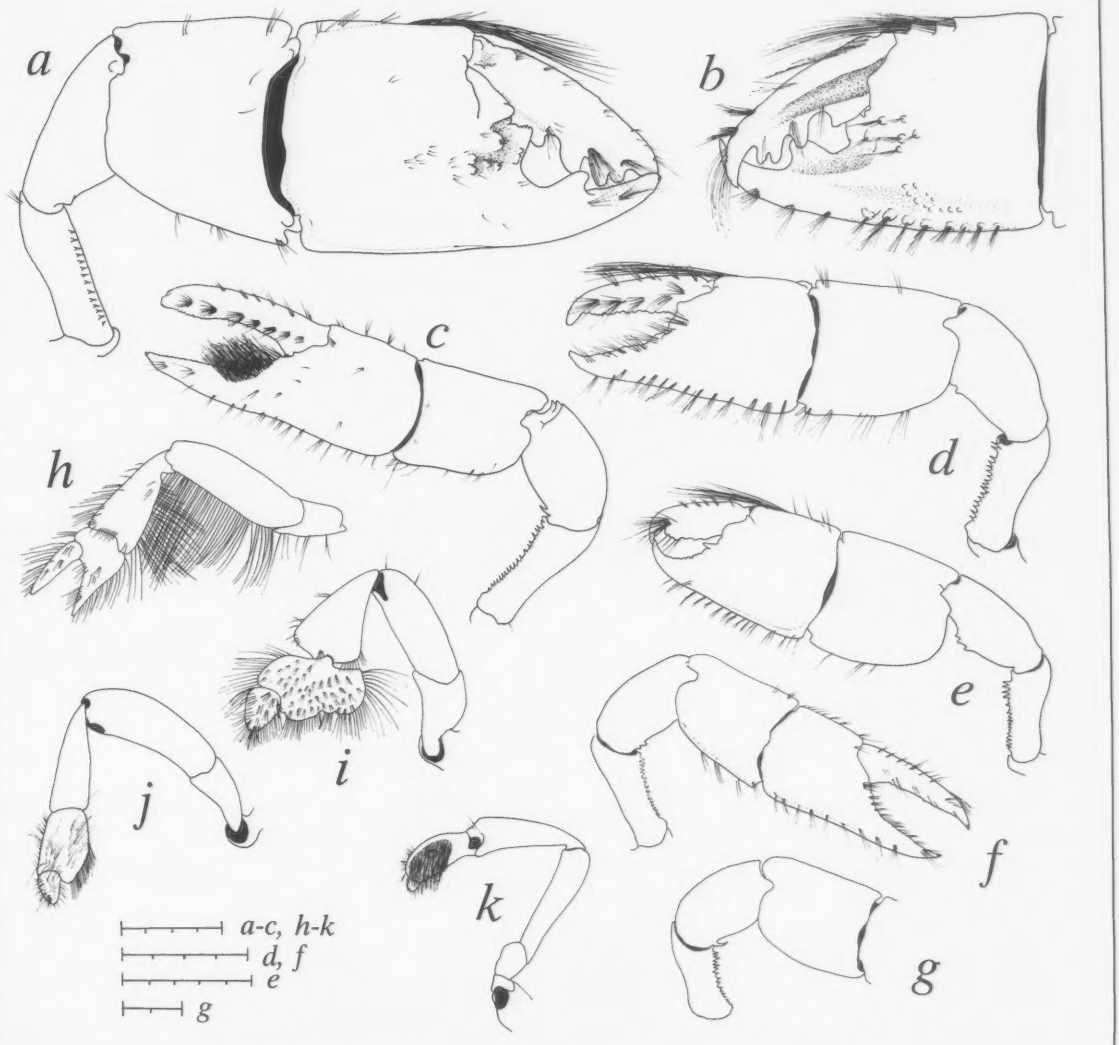

Figure 3

Lepidophthalmus sinuensis new species. (a) Male major cheliped (lateral view); (b) male chela (internal view); (c) male minor cheliped (lateral view); (d, e) female major cheliped (lateral view); (f) female minor cheliped (lateral view); (g) ischium, merus, and carpus of female minor cheliped (lateral view); (h–k) left pereopods: (h) second, (i) third, (j) fourth, (k) fifth. (a–c, h–j) Male CL 11.5 mm; (d, f) female 9.8 mm; (e, g) female CL 9.0 mm; (k) male 10.0 mm. Scales equal 4 mm (a–d, f, h–k), 5 mm (e), and 2 mm (g).

two-segmented (Fig. 4e); distal segment setose, with sinuous anterior margin; basal segment bent in midline at about right angle. Female second pleopod biramous (Fig. 4f), with appendix interna on endopod. Third to fifth pleopods large, strong (Fig. 4g); each pair forming a subcircular fan when linked together by appendix interna; exopod leaf-like, endopod subtriangular.

Telson subrectangular, about 1.4 times as wide as long (Fig. 4b); dorsal surface smooth, with two pairs of tufts of setae (one on anterior half, one near posterolateral angle); lateral margins convex; posterior margin weakly divided into large, medial, broadly rounded lobe, and two rounded lateral lobes. Uropod with protopodite-bearing spine on posterolateral angle;

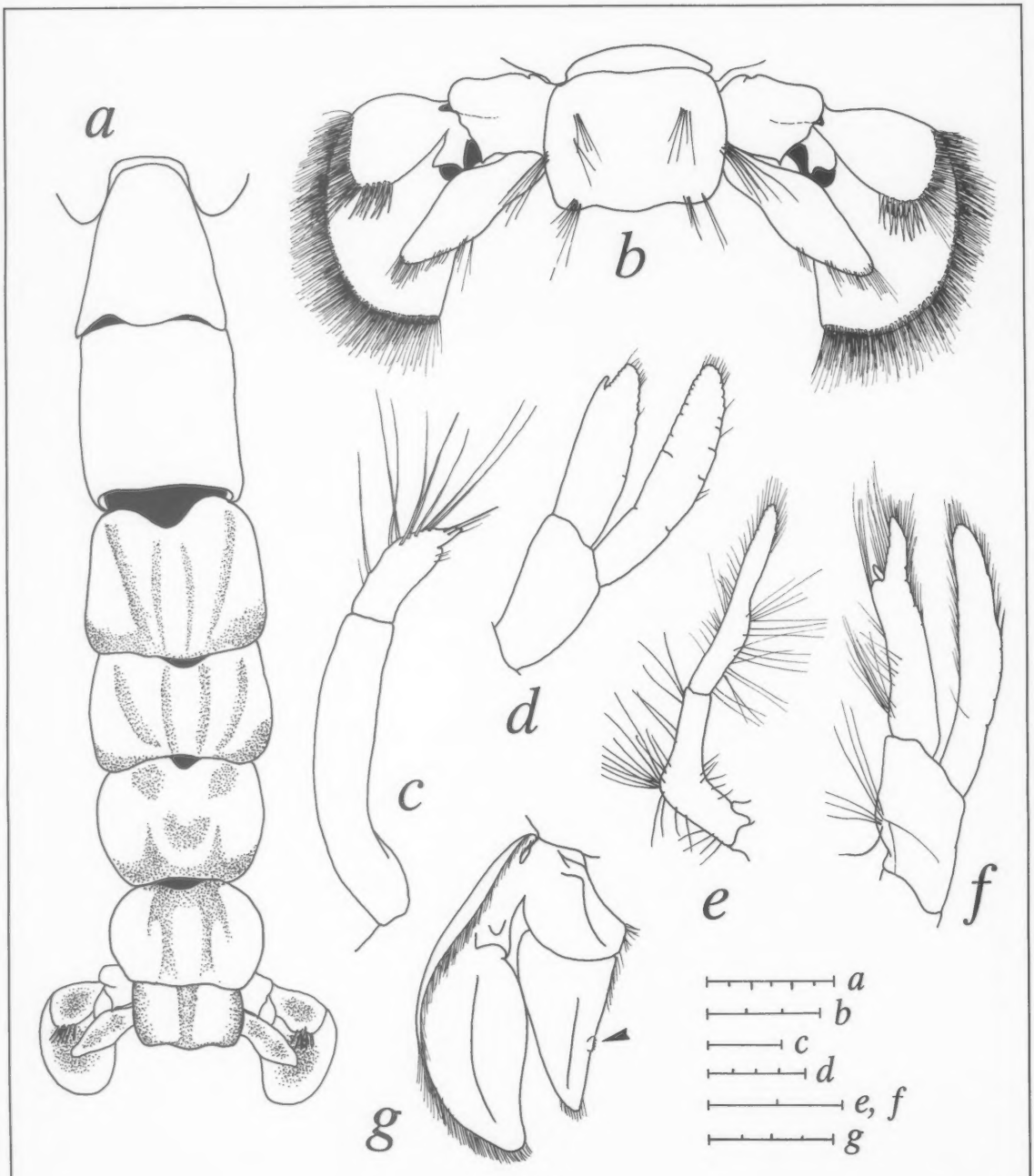

Figure 4

Lepidophthalmus sinuensis new species. (a) Abdomen and tailfan (dorsal view; setae omitted), showing color pattern (stippled areas); (b) telson and uropods (dorsal view); (c) male left first pleopod (lateral view); (d) male left second pleopod (posterior view); (e) female left first pleopod (lateral view); (f) female left second pleopod (lateral view); (g) third left pleopod (posterior view; arrow indicates appendix interna). (a) Female CL 11.3 mm; (b–d, g) male CL 11.5 mm; (e, f) female 9.8 mm. Scales equal 6 mm (a), 3 mm (b), 0.5 mm (c), 4 mm (d, g), and 2 mm (e, f).

endopod narrow, more than 2.5 times as long as broad, distal half slightly bent ventrally; upper exopodal plate shorter and smaller than lower exopodal plate, with rows of long, slender corneous spines on posterolateral margin; lateral margin of exopodal plates with dense setation.

Coloration (Fig. 4a)

In life, carapace transparent except for white frontal region. Chelipeds and pereopods 2–5 white, with densely setose areas brownish or dark orange. Abdomen with somites 1,2 transparent; dorsal surface of somites 3–6 with olive patterns as follows: somite 3,4 with stripes on each side of midline, and one stripe on each side forming a "V"; somite 5 with 3 patches on anterior 2/3 (each patch located on ends of inverted triangle), and band on posterior margin forming a triangle on each side of midline; somite 6 with two stripes on each side of midline. Telson with three olive stripes (one medial, one on each side adjacent to lateral margin). Uropod olive, with darker areas on central part of exopodal plates and endopod.

Distribution

Caribbean coast of Colombia: so far known only from Agrosoledad S.A. shrimp farm, near the mouth of the Sinú River, on the southern coast of the Golfo de Morrosquillo, and south of the farm at a beach near the town of San Bernardo del Viento. Intertidal, and in shrimp ponds at about 1.5 m depth.

Etymology

The specific name is given in honor of the Sinú indians, original inhabitants of the area where the new species was found.

Remarks

The traditional division of the family Callianassidae (Borradaile 1903, de Man 1928a, b) has been under constant criticism by recent authors (de Saint Laurent 1973 and 1979, Manning and Felder 1986, Manning 1987, Sakai 1987). For example, some of the American species that in the past were in the genus *Callianassa* Leach, 1814, are now being reassigned to other genera previously considered junior synonyms of *Callianassa*. This new species is placed in *Lepidophthalmus* Holmes, 1904, a genus recently resurrected by Manning and Felder (In press).

Lepidophthalmus sinuensis can be easily distinguished from the other species in the genus—*L. bocourti* (Milne Edwards 1870) from the eastern Pacific, and *L. louisianensis* (Schmitt 1935) and *L. jamaicense* (Schmitt 1935) from the western Atlantic—by the presence in the new species of large subrectangular projections of the frontal region of the carapace. Other differentiating characters observed in *L. sinuensis* are: the sexual dimorphism shown in the minor cheliped with brush-like setae on the fixed finger of males (lacking in females); the distal segment of the male first pleopod that is weakly divided distally; and the endopod of the uropod that is very slender and bent distally.

Ecological observations

Specimens of *Lepidophthalmus sinuensis* were obtained in penaeid shrimp ponds of about 10 ha each, and in a natural habitat on a beach site west of the shrimp farm. Individuals were easily collected by digging with a shovel or using a yabby pump, a suction device of the type described by Reaka and Manning (1989). Salinities in the ponds ranged from 15 to 25‰. The type of sediment where the new species was found is a very fine grey sand. In one pond with both fine sand and clayish bottom sections, *L. sinuensis* was absent in the clayish section whereas it was abundant in the fine-sand section. Therefore, *L. sinuensis* does not appear to survive in clayish sediment.

The number of burrow openings in the ponds most heavily populated with this callianassid ranged from 1894 to 2093 burrow openings/m^2. Resin casts of the burrows indicate that many have double openings and are Y-shaped. A conservative estimate of the population density in these ponds probably is about half the burrow density (947–1046 individuals/m^2). These densities are among the highest recorded for adult thalassinids. Dworschak (1987) has reported a density of 2420 burrow openings/m^2 of juvenile *Upogebia pusilla* (Petagna), quoting this number as the highest ever reported, and Griffis (1990) found a maximum density of slightly less than 1400/m^2 of juveniles of *Callianassa gigas* Dana.

The great proliferation of *Lepidophthalmus sinuensis* in penaeid shrimp ponds can be attributed, possibly, to one or a combination of the following factors: (1) abundant supply of food due to the high productivity that is artificially produced during the penaeid grow-out cycle (e.g., by addition of fertilizers such as chicken manure, urea, and pelleted food); (2) availability of a large area of undisturbed, stable sand, ideal for the construction of burrows; (3) concentration and increased survival of callianassid larvae in an enclosed area at the time of transition from the planktonic to the benthic stage; and (4) the ability to survive the drying stages of the ponds between grow-out cycles (one pond left dry for 45 days still had a population of live *L. sinuensis*). Callianassids are known to influence sediment

characteristics, benthic communities, and the release of nutrients into the water column (Ott et al. 1976, Posey 1986a,b). The nature of their effect on the penaeid culture is unknown. Based on our observations it appears that, at least during some growing cycles, the activity of *L. sinuensis* can prevent pond-grown penaeid shrimp from reaching a marketable size and weight. However, the exact short-term and long-term effects caused by this new species on the culture will have to be investigated.

Acknowledgments

We thank J.V. Mogollón, J. Araújo, A.P. Serna, and other staff of Agrosoledad S.A. for providing us with the opportunity to study the material, and their help and hospitality during our stay in Cartagena. Our trip to Colombia was possible thanks to the funds provided by Agrosoledad S.A., at the request of J.V. Mogollón, who has been instrumental in the successful development of shrimp mariculture in Colombia. The critical reading of the manuscript by D.L. Felder and R.B. Griffis, and their comments, are gratefully acknowledged.

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Abstract.–The diel pattern in vertical distribution of red drum *Sciaenops ocellatus* larvae was described from plankton collections taken at three depths and three time periods over a 24-hour period during five cruises in inner shelf waters of the northcentral Gulf of Mexico (east Louisiana–Mississippi–Alabama region). Larvae ranging in mean size from 1.7 to 5.0 mm were vertically stratified at both offshore and nearshore locations over bottom depths <25 m. Diel periodicity in vertical stratification was evident in four cruises, with larvae being concentrated higher in the water column during daylight hours than at night. There was no clear relationship between vertical aggregation of red drum larvae and temperature or salinity profiles or prey microzooplankton distribution.

Diel Vertical Distribution of Red Drum *Sciaenops ocellatus* Larvae in the Northcentral Gulf of Mexico

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Diel vertical migration has been observed among the larvae of many taxa of marine fishes in diverse environments ranging from estuaries to the open sea (see Neilson and Perry 1990 for recent review), and under both stratified and well-mixed hydrographic conditions (Ahlstrom 1959, Smith et al. 1978, Kendall and Naplin 1981, Brewer and Kleppel 1986, Perry and Neilson 1988). The most frequently observed pattern of larval movement has been daytime concentration at lower depths with subsequent movement towards the surface at night (Smith et al. 1978, Kendall and Naplin 1981, Boehlert et al. 1985), but the reverse tendency has also been noted (Hempel and Weikert 1972, Boehlert et al. 1985, Yamashita et al. 1985, Sogard et al. 1987, Neilson and Perry 1990). Another pattern is one where larvae are aggregated at depth during daytime but become more dispersed at night (Brewer and Kleppel 1986, Heath et al. 1988). Ontogenetic differences in vertical distribution and migration patterns have frequently been observed (Brewer and Kleppel 1986, Castonguay and McCleave 1987, Stephenson and Power 1988). The adaptive significance of vertical migration remains unknown (Pearre 1979), but some inferred or proposed advantages to fish larvae include maintenance of position relative to prey (Hunter and Sanchez 1976); predator avoidance (Zaret and Suffern 1976); energy conservation through swimbladder inflation at the surface (Hunter and Sanchez 1976); maximization of energy intake through depth-mediated thermoregulation (Wurtsbaugh and Neverman 1988); and enhancement of transport to nursery grounds (Miller et al. 1984, Norcross and Shaw 1984, Boehlert and Mundy 1988). Knowledge of vertical distribution patterns among early life stages is necessary, not only to better understand early ecology but also to improve the design of broadscale surveys for resource and population assessments using the abundance of fish eggs and larvae (Ahlstrom 1959, Stephenson and Power 1988, Perry and Neilson 1988).

Data presented here on diel changes in vertical distribution of red drum *Sciaenops ocellatus* larvae came from an ongoing, comprehensive investigation begun in 1983 into the early ecology (Lyczkowski-Shultz et al. 1988), age and growth (Comyns et al. 1989), and spawning seasonality and biomass (Comyns et al. 1991) of this commercially and recreationally valuable sciaenid in coastal and shelf waters of the northern Gulf of Mexico.

Materials and methods

Ichthyoplankton collections were taken during five, 24-hour cruises in September and October 1984 and 1985 in the general area east of the Mississippi River delta and south of the Mississippi barrier islands over the east Louisiana–Mississippi–Alabama shelf (Fig. 1). Discrete-depth

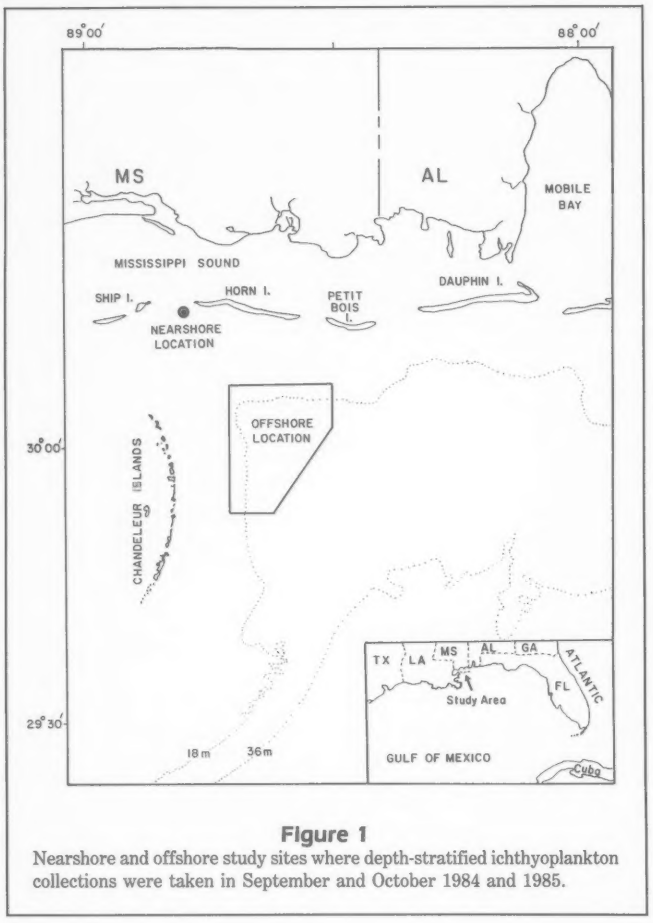

Figure 1
Nearshore and offshore study sites where depth-stratified ichthyoplankton collections were taken in September and October 1984 and 1985.

samples were taken offshore in the vicinity of a "windowshade," subsurface (5 m) current drogue as it was tracked from the ship throughout the duration of a cruise in an attempt to repeatedly sample the same patch of fish larvae and zooplankton (Lyczkowski-Shultz et al. 1988). The drogue traveled, on average, 13 km during a sampling period, typically at varying compass headings over water depths of 18–25 m. During each cruise, collections were usually made during early to late afternoon of the first day, then in the middle of the night (usually prior to midnight), and in the morning (after sunrise) of the second day. In all but one instance, dawn and dusk periods were specifically avoided. Times of sunrise and sunset on sampling dates in September and October 1984 and 1985 ranged from 0543 to 0600 hours, and from 1733 to 1819 hours central standard time (CST), respectively. During three of the five cruises, additional samples were taken at a fixed, shallow water station (12 m) located 15–19 km NNW of the offshore sampling area during midday hours of the second day (nearshore, Fig. 1). Times of high and low tide were determined using predictions for tide stations nearest the offshore sampling sites (NOAA-NOS Tide Tables).

Sampling gear consisted of a 1×1.4 m, multiple-net Tucker trawl with an effective mouth opening of 1 m^2 when fished at a 45° angle, and a double-release mechanism operated manually with messengers. Mean tow speeds varied from 1.5 to 2.5 knots (0.8–1.3 m/s). At the offshore location, three Tucker trawl casts were made during each time period. A cast consisted of all three 333-μ mesh nets being fished in horizontal 5-min hauls at one nominal depth level at a time. These sampling depths were 1, 5, and, most typically, 11 or 12 m. At the nearshore location, each of the three nets were fished at 1, 3, and 7 or 9 m, but the nets were of different mesh sizes: 333, 505, and 760 μ. Offshore catch data from the three net samples at each depth were pooled for analyses for cruises 84-9-1, 84-10-1, and 85-9-1, even though only net 2 was both opened and closed at depth. Contamination in nets 1 and 3 was considered to be minimal due to the relatively short time for their deployment and retrieval, less than 30 seconds in total. Comparison of catches from the three nets indicated that contamination had not seriously affected our results, as there was little to no overlap among adjacent sampling depths in the range of observed densities (as measured by each of the three nets) per sampling period (Fig. 2). Catch data from all three nets of different mesh sizes at the nearshore site were combined since sampling effort, i.e., number of samples per mesh size at each depth, was the same. Due to time constraints, only net 2 samples (the 333-μ mesh net at the nearshore site) were sorted from cruises 84-9-2 and 85-10.

Fishing depth was monitored throughout each tow via the depth sensor of an electronic conductivity/temperature/depth probe package (CTD) which was mounted 0.5 m above the trawl frame on the conducting/towing cable. Except for the nearsurface or 1 m depth stratum, actual sampling depths exceeded nominal depths by 0.5 m. Target or nominal sampling depths were maintained throughout each tow by adjusting the amount of wire out.

Flowmeters in each net measured volume filtered which generally ranged between 200 and 300 m^3.

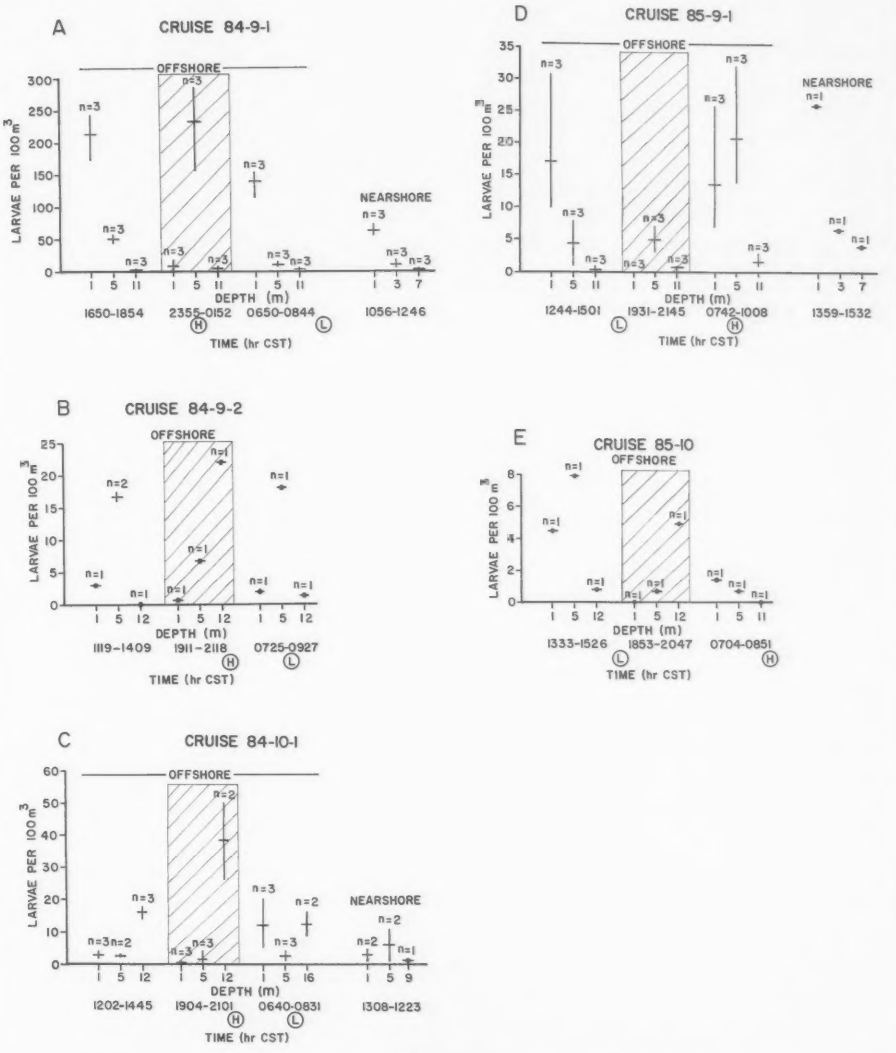

Figure 2

Mean and range in density of red drum larvae *Sciaenops ocellatus* by sampling depth and time at offshore and nearshore sites during cruises in 1984 and 1985. n = number of collections per sampling period. Crosshatching denotes nighttime observations. Encircled H and L symbols mark the approximate times of high and low tide.

Vertical profiles of temperature and salinity prior to sample collection were obtained with the CTD.

Ichthyoplankton samples were preserved at sea in 5–10% formalin and were later (1 week to 6 months) transferred to 70% ethanol for final preservation. In the laboratory, all larvae were removed from either the entire sample or from a one-half aliquot which was obtained using a Motoda plankton splitter (Van Guelpen et al. 1982). Standard length (SL) of larvae was measured to the nearest 0.1 mm at 12× using a stereomicroscope. Larval densities are reported as number per 100 m^3.

Zooplankton samples were collected by pumping water up from the same depths as ichthyoplankton

collections with a 38 L/min capacity diaphram pump and filtering approximately 0.3–0.5 m^3 through nested 63 and 25 μ mesh nets on deck. Zooplankton samples were preserved in 5% formalin. The average time between collection of fish larvae and zooplankton was 2.5 hours, with values ranging between 21 minutes and 4 hours.

Statistical analysis of diel vertical patterns in larval red drum abundance was conducted using nonstandard, chi-squared, goodness-of-fit procedures (McCleave et al. 1987). First, the standardized residual of larval density at each depth was calculated,

$$SR_i = \frac{(N_i - E_i)}{\sqrt{E_i}}$$

where N_i = observed catch at depth i, and E_i = expected catch at depth i. E_i was calculated by multiplying the total number of red drum larvae caught during a time period (all depths combined) by the proportion of total fishing effort at that depth, i.e., the volume filtered at that depth divided by the total volume filtered during the time period. The sum of squared SR_i's yields the chi-squared (χ^2) statistic for testing the null hypothesis that within a single time period the density of red drum larvae is uniform with depth. A second null hypothesis—that the vertical distribution of larvae remains unchanged over the diel cycle, i.e., among the three sampling periods—was investigated using the chi-squared test for heterogeneity (a nonstandard, goodness-of-fit test; Sokal and Rohlf 1981). This was accomplished by subtracting the χ^2 value for the combined data set (three time periods) from the sum of the individual χ^2's for each time period.

Results

Depth-stratified ichthyoplankton collections during afternoon, night, and morning, over a 24-hour period during five cruises, were examined for patterns in vertical distribution of red drum larvae. Larvae were vertically stratified in both offshore and nearshore waters (Fig. 2). Larvae were usually more abundant at 1 and/or 5 m than at 11, 12, or 16 m at the offshore location, and than at 7 or 9 m at the nearshore location. In two of the three cruises in which both offshore and nearshore sites were sampled, the depth of greatest abundance (at a comparable time period) was the same at both nearshore and offshore sites (Fig. 2A, D).

Vertical stratification at the offshore location appeared to have a diel component in four cruises (Fig. 2A, B, D, E). The most consistent diel pattern was a decrease in abundance, relative to afternoon values, at 1 m and a relative increase at 5 or 11–12 m during nighttime hours. The following morning, abundance at 1 and/or 5 m was higher than the nighttime values at those depths. During cruise 84-9-2 the diel shift in maximum abundance occurred between 5 and 12 m, with abundance at 1 m remaining relatively constant throughout the 24-hour period (Fig. 2B). Mean density of larvae during cruise 84-10-1 was highest at 12 m during both afternoon and night, but in the morning maximum density values were observed at both 1 and 16 m (Fig. 2C).

The most distinct pattern of vertical stratification was observed in cruise 84-9-1 where the center of abundance of red drum larvae shifted from 1 to 5 m and back to 1 m over the three time periods, with no overlap in mean density or range in densities among adjacent depths within a sampling period (Fig. 2A). Mean density at 1 m in the afternoon was remarkably similar to the mean density at 5 m at night, 214.5 vs. 234.5, but by morning of the next day maximum abundance had declined to 141.0. Although vertical stratification was evident in the other three offshore data sets, the diel pattern was less distinct.

Nonstandard, chi-squared goodness-of-fit analyses were used to test two null hypotheses (McCleave et al. 1987): that (1) red drum larvae were homogeneously distributed over the three sampling depths, and (2) the vertical distribution of larvae remained unchanged over three sampling times spanning a diel cycle. In 17 of 18 cases, including both offshore and nearshore sites, null hypothesis 1 was rejected at the 0.01 significance level (Tables 1 and 2). In all five data sets from the offshore site, null hypothesis 2 was also rejected at the 0.01 significance level, i.e., larval depth distribution did not remain the same among the sampling periods (Table 1).

The sign and magnitude of standardized residual deviations, SR_i values, were examined to determine the diel pattern in vertical distribution of red drum larvae (Table 1). In four of five cruises, the depth of greatest larval abundance was higher in the water column during afternoon hours than at night (Fig. 2). In two cruises (84-9-1 and 84-9-2), the depth of greatest larval abundance on the following morning was the same as on the preceding afternoon and, therefore, higher in the water column than on the preceding night. In one cruise (85-9-1), although the depth of greatest abundance (5 m) in the morning was the same as at night, abundance at 1 m (depth of greatest abundance during the preceding afternoon) had increased relative to the nighttime value. The morning sampling period of cruise 85-10 was the only case where larvae were homogeneously distributed throughout the water column. During the only cruise (84-10-1) in which depth of greatest larval abundance was the same in afternoon

Table 1

Analyses of the null hypotheses: (1) red drum larvae are homogeneously distributed over three sampling depths, and (2) the vertical distribution of larvae is similar over three sampling times spanning a diel cycle. Data from five cruises from offshore Mississippi waters in September and October, 1984 and 1985. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

	Afternoon (1650–1854 hrs)				Night (2355–0152 hrs)				Morning (0650–0844 hrs)				Times combined		
Depth	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-1, 13–14 September 1984															
1	835	1807	757	+38	647	63	587	−22	722	993	336	+36	2863	1680	+29
5	610	308	553	−0	916	2217	830	+48	741	84	345	−14	2609	1728	+21
11	896	8	812	−28	1011	53	917	−28	938	41	437	−19	102	2166	−44
Total	2341	2123			2575	2333			2401	1118					
Chi-square χ^2				2360**				3600**				1841**			3248
$\chi^2_{0.01,\ 2df} = 9.21$															
$\chi^2_{het} = \chi^2_{aft} + \chi^2_{night} + \chi^2_{morn} - \chi^2_{comb} = 7801 - 3248 = 4553^{**}$															
$\chi^2_{0.01,\ 4df} = 13.28$															
	Afternoon (1119–1409 hrs)				Night (1911–2118 hrs)				Morning (0725–0927 hrs)				Times combined		
Depth	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-2, 26–27 September 1984															
1	415	12	33	−0.4	382	2	36	−6	209	4	17	−3	18	85	−7
5	432	72	34	+6	387	26	36	−2	332	60	27	+6	158	97	+6
11	208	0	17	−4	346	76	32	+8	307	4	25	−4	80	73	+0.8
Total	1055	84			1114	104			847	68					
χ^2				58**				94**				69**			92
$\chi^2_{het} = 220 - 92 = 128^{**}$															
	Afternoon (1202–1445 hrs)				Night (1904–2101 hrs)				Morning (0640–0831 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-10-1, 10–11 October 1984															
1	986	30	73	−5	741	2	113	−10	700	83	61	+3	115	221	−7
5	978	28	72	−5	752	10	115	−10	769	19	67	−6	57	228	−11
12(16)	998	160	73	+10	833	344	128	+19	982	112	86	+3	616	287	+19
Total	2962	218			2325	356			2451	214					
χ^2				154**				573**				50**			557
$\chi^2_{het} = 777 - 557 = 220^{**}$															
	Afternoon (1244–1501 hrs)				Night (1931–2145 hrs)				Morning (0742–1008 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 85-9-1, 11–12 September 1985															
1	721	131	47	+12	666	0	13	−4	677	92	70	+3	223	130	+8
5	779	36	51	−2	652	34	13	+6	636	130	66	+8	200	130	+6
11	1103	2	72	−8	667	6	13	−2	984	16	102	−9	24	187	−12
Total	2603	169			1985	40			2297	238					
χ^2				223**				51**				142**			246
$\chi^2_{het} = 416 - 246 = 170^{**}$															
	Afternoon (1333–1526 hrs)				Night (1853–2047 hrs)				Morning (0704–0851 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 85-10, 10–11 October 1985															
1	224	10	10	+<0.1	305	0	6	−2	286	4	2	+1	14	18	−0.9
5	254	20	11	+3	285	2	5	−1	286	2	2	−<0.1	24	19	+1
12(11)	240	2	11	−3	284	14	5	+4	281	0	2	−1	16	18	−0.5
Total	718	32			874	16			853	6					
χ^2				14**				22**				4ns			3
$\chi^2_{het} = 400 - 3 = 37^{**}$															

Table 2

Analyses of the null hypothesis: red drum larvae are homogeneously distributed over three sampling depths at the nearshore site. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

Cruise 84-9-1					Cruise 84-10-1					Cruise 85-9-1				
Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i
1	757	469	169	+23	1	706	20	35	−3	1	591	84	53	+4
3	847	94	189	−7	5	1025	81	51	+4	3	275	18	25	−1
7	1025	25	229	−13	9	393	4	19	−4	7	498	20	45	−4
Total	2629	588				2124	105				1364	122		
χ^2				761**					37**					34**

$\chi^2_{0.01, 2df} = 9.21$

and night sampling periods, there was an increase in abundance at 1 m in the morning hours with mean densities at 1 and 16 m being identical.

Size composition of red drum larvae within cruises remained relatively constant except during cruise 85-9-1 when mean size in the morning was much smaller than during two previous sampling periods (Table 3). Red drum larvae did not appear to be depth-stratified by size.

Vertical profiles of temperature and salinity taken just prior to sampling during each of the five cruises consistently showed the water column to be well-mixed (Fig. 3). There was no evidence of a well-defined or persistent thermocline to which red drum larvae might orient. Mean temperature averaged over sampling depths was 3°C higher during cruises 84-9-1&2 and 85-9-1 than during cruises 84-10-1 and 85-10. Salinity varied somewhat more throughout the water column than did temperature but usually differed no more than 2–3 ppt between September and October observations. Isohaline conditions generally prevailed within the upper 12 m of the water column during all cruises except 84-9-1, when a difference in salinity of 5 ppt between the surface and 12 m was observed throughout all three sampling periods (Fig. 3A). Yet the same general pattern in vertical stratification of red drum larvae was evident within that salinity gradient as was observed under more isohaline conditions. There was also no consistent relationship between tidal stage and vertical position of larvae (Fig. 2). This was especially evident during cruises 84-9-1 and 85-9-1 when red drum larvae showed the same general pattern in vertical distribution under the opposite stage of the tide.

Moonlight intensity as influenced by moon phase, time of moonrise, and presence/absence of cloud cover did not appear to explain similarities or differences among cruises in nighttime vertical distribution of red drum larvae. Cruises 84-9-2, 85-9-1, and 85-10 were all conducted within 2 to 3 days of the new moon, i.e., when moonlight was at a minimum. Cruises 84-9-1 and 84-10-1 were both conducted 2 to 3 days after the full moon, on cloudless nights with moonrise occurring early in the evening, i.e., when moonlight was near maximum.

Table 3

Mean standard length in millimeters (standard error of the mean in parenthesis) of red drum larvae at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters.

Depth	Afternoon	Night	Morning
	Cruise 84-9-1		
1	2.8 (0.02)	2.7 (0.03)	2.9 (0.02)
5	2.7 (0.02)	2.7 (0.02)	2.6 (0.05)
11	2.8 (0.12)	2.7 (0.05)	2.6 (0.06)
	Cruise 84-9-2		
1	2.9 (0.13)	1.8 (—)	2.3 (0.48)
5	2.5 (0.04)	2.9 (0.04)	2.7 (0.08)
12	—	2.9 (0.05)	2.6 (0.68)
	Cruise 84-10-1		
1	4.7 (0.31)	3.8 (—)	4.4 (0.15)
5	4.0 (0.24)	4.6 (0.27)	4.3 (0.29)
12 (16)	3.9 (0.11)	4.5 (0.11)	4.0 (0.09)
	Cruise 85-9-1		
1	4.7 (0.05)	—	1.9 (0.13)
5	4.4 (0.11)	4.6 (0.20)	2.1 (0.14)
11	4.6 (—)	5.0 (0.31)	1.7 (0.02)
	Cruise 85-10		
1	3.7 (0.15)	—	3.3 (0.16)
5	3.4 (0.11)	4.6 (—)	4.4 (—)
12 (11)	1.3 (—)	3.6 (0.11)	—

The vertical distribution of prey microzooplankton, based on a single collection per depth, was compared with the depth of maximum abundance of red drum larvae at the offshore location (Table 4). Microzooplankton were grouped into three categories based on examination of larval gut contents, net-caught zooplankton, and statistical comparisons of diet and prey availability

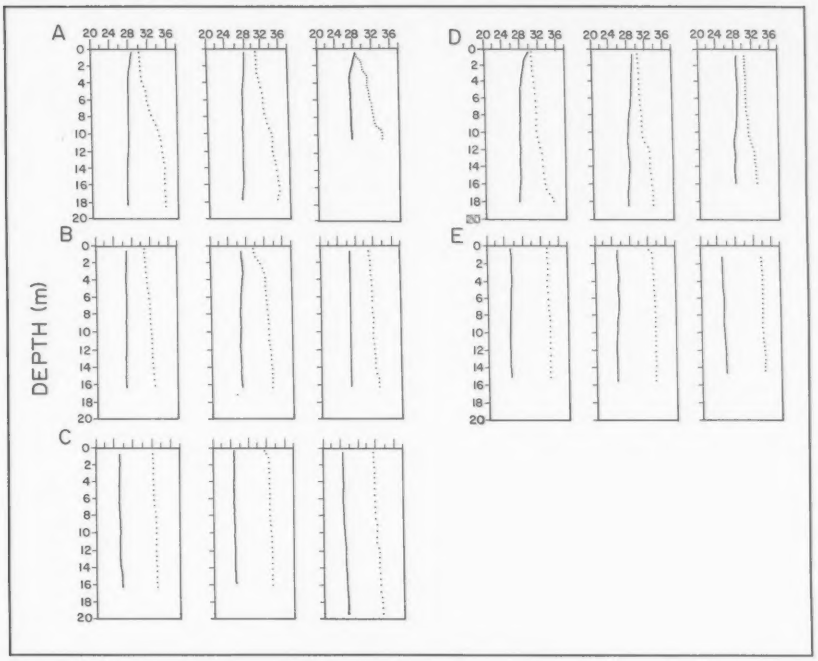

Figure 3
Vertical profiles of temperature (°C, solid line in each plot) and salinity (ppt, dotted line in each plot) during afternoon (left plot), night (center plot), and morning (right plot) sampling periods from cruises: (A) 84-9-1, (B) 84-9-2, (C) 84-10-1, (D) 85-9-1, (E) 85-10.

Table 4
Density of prey microzooplankton (n/L) at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters. Asterisks indicate depth of highest observed red drum density for that time period. A = density of "preferred" prey; B = density of crustacean nauplii; C = density of total prey zooplankton in the size range 63–230 μ maximum width (excluding appendages).

	Afternoon			Night			Morning		
Depth	A	B	C	A	B	C	A	B	C
Cruise 84-9-1									
1	7	81	216*	2	109	189	1	53	97*
5	11	133	275	5	187	313*	1	57	104
11	4	67	91	6	113	172	8	127	215
Cruise 84-9-2									
1	24	44	268	32	97	258	14	137	194
5	22	123	352*	27	139	298	16	118	263*
12	23	61	370	24	79	168*	10	780	182
Cruise 84-10-1									
1	—	—	115	—	—	103	—	—	101*
5	—	—	115	—	—	126	—	—	133
12 (16)	—	—	77*	—	—	186*	—	—	303*
Cruise 85-9-1									
1	10	38	84*	30	75	209	5	53	88
5	23	59	178	21	115	274*	17	90	181*
11	7	71	129	20	86	198	20	60	180
Cruise 85-10									
1	<1	22	72	<1	8	22	<1	22	62*
5	1	36	79*	2	12	45	0	18	46
12 (11)	0.6	23	83	3	27	159*	6	17	128

(Lyczkowski-Shultz et al. 1988). Results of these analyses led to the separation of red drum larvae into three size categories: <2mm, >2 to ≤4mm, and >4mm, based on diet composition. Column A in Table 4, "preferred" prey, is the combined observed density, from field collections, of those taxa of calanoid and cyclopoid copepods found to most uniquely describe the diet of larvae of the size indicated by the mean lengths listed in Table 3. Crustacean nauplii, column B in Table 4, were the most ubiquitous prey found in red drum larvae of all sizes, and column C is the density of all potential prey items within the size range 63–230 μ, i.e., the total size range of prey found to be ingested by red drum larvae.

In only 6 of 15 vertical data sets did the depth of maximum abundance of larvae coincide with the depth of maximum abundance of their prey. Of the 10 daytime vertical data sets when red drum larvae were most likely to be feeding (Lyczkowski-Shultz et al. 1988), the depth of maximum abundance of red drum larvae coincided with the depth of maximum abundance of their prey in only three instances. In one of those instances, the morning sampling period of cruise 84-10-1, red drum larvae were equally abundant at the depths of lowest and highest observed microzooplankton densities.

Discussion

Red drum larvae ranging in mean size from 1.7 to 5.0 mm were vertically stratified in waters of less than 25 m of the northcentral Gulf of Mexico. Larvae were most frequently found to be concentrated higher in the water column during the day than at night in vertically well-mixed coastal and inner shelf waters. The lack of a consistent correspondance between depth of maximum larval red drum abundance and depth of maximum prey microzooplankton abundance was not unexpected since, in general, high prey densities (>100 organisms/L) were observed throughout the water column. Brewer and Kleppel (1986) likewise found no correspondance between prey densities and the daytime vertical distribution of northern anchovy and white croaker larvae. The time lag (2–3 hours) between the collection of ichthyoplankton and zooplankton samples may have affected our results if the spatial coincidence of larvae and prey occurred over a shorter time interval than the interval between samples.

It is feasible to assume that red drum larvae maintain this pattern of vertical distribution by responding to diel changes in illumination. In their recent review, Neilson and Perry (1990) concluded that light is important in mediating diel vertical migration in many fishes throughout ontogeny. Diel variations in the distribution patterns of young fishes are associated with activity, phototaxis, and brightness discrimination (Blaxter 1969). Blaxter (1973) was able to induce vertical migration in herring and plaice larvae by varying ambient light levels in the laboratory or by exposing larvae to natural conditions of dawn and dusk. We have observed that 3-5 day-old red drum larvae in the laboratory are positively phototactic and tend to concentrate at the very surface of 4 L rearing containers with artifical lighting directly overhead. Larvae were not observed under dark conditions. The range in vertical movement, 5–12 m, required to maintain the diel distribution pattern observed in this study is theoretically possible if the swimming capabilities of 2–5 mm drum larvae are similar to those of other fish larvae, i.e., with cruising speeds of 2–3 body lengths per second (Blaxter 1969, Theilacker and Dorsey 1980). The role of the swimbladder, clearly visible in red drum larvae by at least 2 mm, in "depth holding" (Blaxter 1986) is not known. A comprehensive explanation of how red drum larvae maintain vertical position in the shallow depths of their early nursery grounds requires a more thorough knowledge of early sensory and locomotor capabilities in this species.

The pattern of diel vertical distribution displayed by red drum larvae, implying nocturnal descent, has been termed "reverse diel vertical migration" and has been observed by various workers (Wood 1971, Richards and Kendall 1973, Ohman et al. 1983, Kuwahara and Suzuki 1984, Boehlert et al. 1985, Yamashita et al. 1985, Leis 1986, Sogard et al. 1987). From their review of the literature on vertical migration among fishes, Neilson and Perry (1990) found this pattern to be less common than nocturnal ascent, often associated with similiar movements of prey species, and implicated in reducing predation pressure. Yamashita et al. (1985) attributed this distribution pattern among Japanese sand lance larvae to daytime feeding activity in the upper levels of the water column. The authors suggested that when feeding stops after dark, larvae become relatively inactive and gradually sink to greater depths; with the return of daylight, feeding resumes and larvae move upward.

Activity levels among fish larvae are associated with diurnal light changes and phototaxis (Blaxter 1969). The threshold light intensity found to initiate vertical movement of herring and plaice larvae in the laboratory was similiar to the light threshold for feeding (Blaxter 1986). It would be advantageous for larvae such as red drum living in turbid coastal waters to move into more brightly illuminated levels to feed, given the poor visual acuity and limited retinomotor response capabilities (light/dark adaptation) found in the early larvae of most marine fishes (Blaxter 1969).

Prior to this study, vertical distribution of red drum larvae in the Gulf of Mexico had only been described for estuarine/bay systems. Peters and McMichael (1987) never found red drum larvae at the surface during daytime hours in 1 m plankton net collections in Tampa Bay, Florida, where red drum larvae were found to be most abundant nearest the bay mouth. Collections at the bay mouth, however, were taken only at night during a flood tide. The most extensive data on vertical distribution of red drum larvae comes from Aransas Pass tidal inlet on the southern Texas coast where vertical position appears to be influenced by direction of tidal flow (Holt et al. 1989). Further observations and data indicate that high surface densities are generally associated with flooding conditions and/or oceanic water, while high bottom densities occur during ebbing conditions and/or in bay water (S.A. Holt, Mar. Sci. Inst., Univ. Texas at Austin, Port Aransas, TX 78373, pers. commun. Aug. 1990). Tides along the south Texas coast are principally diurnal, and during the red drum spawning season, the flood tide generally occurs at night while the ebb tide occurs during the day.

The relative proportion of the larval red drum population occurring below maximum sampling depths during our study is unknown, but presumed to be small (Comyns et al. 1991). Observations taken during a yearlong survey of Mississippi Sound and adjacent coastal

waters also suggest that red drum larvae, at least during daytime and under flooding conditions, do not occur in large numbers in nearbottom waters of the study area (Lyczkowski-Shultz and Richardson, unpubl. data). Monthly daytime plankton collections were taken from November 1979 to October 1980 at 16 sites inside Mississippi Sound (mean depth 3.9 m), in three tidal passes (mean depth 7.2 m), and at two sites outside the Sound located 7.4 km south of Horn and Petit Bois Islands (mean depth 15.6 m). At each location two depth strata, surface to midwater and midwater to within 0.5 m of the bottom, were sampled separately with stepped oblique hauls of an opening/closing meter net (Lyczkowski-Shultz et al. 1990). Red drum larvae ranging in size from 2.0 to 8.5 mm from 88 collections at all sampling sites combined were more than twice as abundant in the upper half of the water column as in the lower half. This difference was even more pronounced at the two sites outside the Sound where the mean density of larvae (number/100 m^3) was 12.3 in the surface stratum and 4.0 in the bottom stratum. Unlike red drum larvae, the larvae of Atlantic croaker *Micropogonias undulatus* and spotted seatrout *Cynoscion nebulosus* from this same series of collections were more than twice as abundant in the lower half of the water column as in the upper half.

Although the Mississippi Sound and adjacent waters survey was not designed to investigate the role of tide on the distribution of red drum larvae, data from the three barrier island pass stations did tend to support the Aransas Pass inlet observations. Ebbing flow prevailed during sampling at the pass stations only twice during the months when red drum larvae were collected (September and October), and the only instance when drum larvae were more abundant in nearbottom (9 larvae/100 m^3) than in surface waters (0 larvae) occurred during one of those ebb tide collections in Petit Bois Pass. The density of red drum larvae at the offshore station directly south of this pass and under the same ebbing tide, however, was almost three times higher in the surface stratum than in the nearbottom stratum. Our observations from coastal and inner shelf waters during 1984 and 1985 also indicate that tidal stage has little influence on vertical position of red drum in offshore waters.

The vertical distribution of larvae found on cruise 84-10-1 was the only data set that deviated from this generalized pattern. Larvae were concentrated at 12 m during both afternoon and night sampling periods. On the morning of the second day, mean density at 1 and 16 m was the same, suggesting that only a portion of the larval red drum population had moved upward or that the population was still in the process of moving upward. Collections during this cruise contained many large larvae (>4.0 mm) and the night-to-day catch ratio indicated that twice as many larvae were caught during nightime as in daytime collections. Gear avoidance alone does not explain the absence of larvae at 1 and/or 5 m early in the cruise. The catch ratio for cruise 85-9-1, when larvae >4.0 mm were numerous in collections (Table 3), was 0.2, indicating that more larvae were captured in the daytime.

Local conditions in biological and physical environments can modify diel vertical migration patterns among fish larvae (Neilson and Perry 1990). The "anomalous," deeper daytime distribution of red drum larvae early in cruise 84-10-1 may have been related to local environmental conditions. There are no data on which to assess the influence of predator distributions during this study, and there was no apparent coupling between red drum larvae and their prey. Variations in tidal phase or times of sunrise and sunset do not account for the different pattern observed during cruise 84-10-1. Tidal phase was about the same during all three cruises in 1984 (Fig. 2), and the differences in time of sunrise and sunset between sampling dates in September and October were small, only 17 and 36 minutes, respectively. Temperature and salinity profiles during this cruise were indicative of a homogeneous water column.

Meterological conditions may have been in part responsible for the distribution pattern observed during cruise 84-10-1. On both the day preceding and the first day of this cruise, skies were overcast and rainy with winds in excess of 15 knots; whereas on the morning of the second day, and during all other cruises of our study, skies were clear and winds generally were light. Heath et al. (1988) investigated the effects of sea-surface light intensity and wind stress on the vertical distribution of herring larvae. He found larval aggregation at depth to vary at about the same frequency as light intensity, i.e., diurnally; whereas mean population depth (center of density) was most influenced by wind-induced mixing, with larvae being found deeper in the water column at times of higher wind stress. Weather conditions may also have affected the vertical distribution pattern observed during cruise 84-9-2. Winds during this cruise were light, but for prior days winds had been greater than 10 knots. Although larvae were more abundant higher in the water column in the daytime than at night, the diel changes in maximum abundance extended deeper than in the previous cruise, occurring between 5 and 12 m, instead of 1 and 5 m (Fig. 2B).

Characterization of any dynamic biological process such as vertical migration is constrained by sampling design and gear (Pearre 1979). Plankton nets do not, for example, yield information on whether movement within a population is synchronous or asynchronous, or whether rates of ascent and descent differ among segments of the population. Contradictory observations

or deviations from a proposed pattern can result from sample "snapshots" being taken at different times of an ongoing process. Use of a current drogue as a reference marker for the collection of plankton samples in our study increased the probability of staying with, and repeatedly sampling, a particular patch of red drum larvae. This was clearly the case in cruise 84-9-1, when both larval abundance and size composition remained essentially unchanged throughout the duration of the cruise. Use of a reference marker does not, however, invariably ensure that a particular population will continue to be sampled. During cruise 85-9-1, the change in size composition of larvae in the morning sampling period indicated that a different patch of larvae was being sampled. Nonetheless, a drifting or Lagrangian sampling design would be more likely to yield an accurate description of diel vertical movements than the more typical ichthyoplankton survey design where collections are made at varying times and locations. Sampling designs based on fixed stations are more appropriate for resource surveys when observations from large geographic areas encompassing all or most of a species' spawning grounds are needed to estimate spawner biomass from the abundance of eggs and/or larvae.

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Trophic Relationships within the Antarctic Demersal Fish Community of South Georgia Island

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Abstract.–Knowledge of trophic relationships is vital to understanding any ecological community. The trophic relationships of Antarctic demersal fish are poorly known and have been described quantitatively by only a few researchers.

Gut contents were analyzed on over 300 stomachs from fish collected during the 1987–88 AMLR ground fish survey of South Georgia I., Antarctica. All fish were collected with a bottom trawl during the austral summer. Fifteen species of demersal fish (including those of commercial value) were collected. Similarity analysis was applied to the diet information to describe trophic relationships in the South Georgia community.

The most abundant species of the South Georgia demersal fish community were classified into three groups based on summer diets. The largest group contained species heavily dependent on krill *Euphausia superba*, and included *Champsocephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consisted of krill. The third group contained a loose association of species which feed on benthic organisms more than did other fish species in the community. *Notothenia gibberifrons* and *Notothenia squamifrons* were the important commercial species in this group.

Krill was found to be the most important prey species to the fish in the South Georgia system. However, based on the analysis of diet overlap, competition appeared to be unimportant in this community during the austral summer.

Selective reduction of populations within the fish community by fishing may have widespread repercussions. Many of the commercially valuable species feed on other fish species which in turn feed on krill or benthic organisms. The relatively simple but highly interconnected food web in the South Georgia system may have a lower potential for fish yield than previously thought.

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The Antarctic ecosystem has been physically isolated from the rest of the world for at least the last 30 million years, since the Drake passage opened as South America moved away from Antarctica (Kennett 1982: 726) and probably longer (Regan 1914). The fish assemblage of this region appears to be the result of evolutionary radiation from a limited fauna that was present in the region when Antarctica separated from Australia (Eastman 1985, Kock 1985b). Over 60% of the species and 90% of the individuals belong to four families in the suborder Notothenioidei, and 95% of the species in this group are endemic to the Antarctic region (DeWitt 1971, Kock 1985b). The four dominant families are the Antarctic cods (Nototheniidae), dragonfish (Bathydraconidae), icefish (Channichthyidae), and spiny plunderfish (Harpagiferidae). These fish are generally sedentary, benthic forms found on the Antarctic continental shelves (Norman 1938). An international fishery has developed for larger members of these families, especially in the region around South Georgia I. (Fig. 1) (Kock 1986).

South Georgia is located just south of the Antarctic Convergence and is surrounded by a narrow, relatively shallow continental shelf. The physical oceanography of the region is very complex (Foster 1984) and may contribute to the high productivity and abundance of krill (Hempel 1985).

There is a high degree of endemism in Antarctic fishes (DeWitt 1971). The assemblage of fish species that has evolved in the Southern Ocean is well adapted to the Antarctic environment (Eastman 1985). However, the fish community in the South Georgia area appears to be changing, possibly in response to the fishing pressure that it has experienced over the past two decades (Kock 1985b and 1986, McKenna and Saila 1991). Exploited South Georgian stocks have been declining since the late 1970s (Kock 1985b and 1986, Gabriel 1987). In the early 1970s, the commercial trawl fishery was supported mostly by the catch of marbled rockcod *Notothenia rossii*, which yielded hundreds of thousands of tons each season (Kock 1986). By 1985, the stock was estimated to be less than 10% of its pristine size (Kock 1985b). The fishery is presently supported by catches of mackerel icefish *Champsocephalus gunnari*, but its decline is also evident (Kock 1986, McKenna and Saila 1989). Abundance estimates of other species in the South Georgia region decreased by as much as two orders of magnitude between 1975–76 and 1980–81 (Kock et al. 1985a).

The community structure has changed with decreases in stock sizes (McKenna and Saila 1991). There has been a significant shift from a community dominated by a few large-bodied species to fewer, mostly small-bodied species with more equitable abundances.

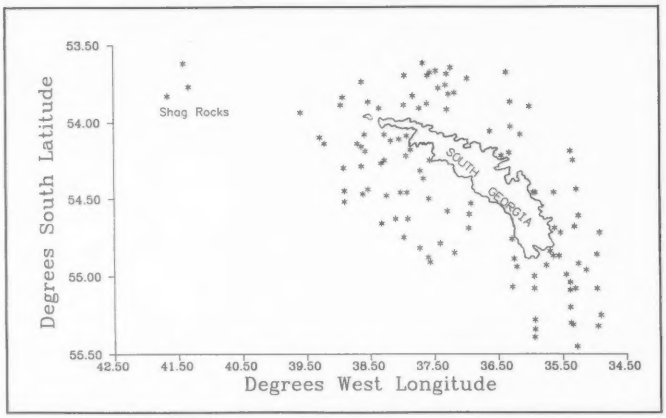

Figure 1
Location of stations sampled around South Georgia I., Antarctica, by the 1987–88 AMLR demersal fish survey.

To effectively manage fish stocks, it is necessary to understand the impact of fishing on the fish community. This includes understanding interspecific relationships among fish and with other organisms in their environment. Knowledge of trophic relationships is necessary to describe these ecological links (Edwards and Bowman 1979, Grosslein et al. 1980, Langton 1983, Sissenwine 1984).

A number of other studies have examined the diets of Antarctic fish (Holloway 1969, Permitin and Tarverdieva 1979, Yukhov 1971, Rakusa-Suszczewski and Piasek 1973, McCleave et al. 1977, Moreno and Osorio 1977). Everson (1984b) reviews the feeding ecology of Antarctic fishes. However, few of these studies have quantitatively measured the interspecific overlap of diets. The most extensive work is that of Targett (1981) who gave a quantitative description of the community structure and trophic relationships of demersal fish around three Antarctic islands. However, his collections were made with a small net (3 m) (not easily compared with those used commercially, (17–18 m)) and only two stations were sampled in the South Georgia I. region late in the autumn of 1975.

Targett's work emphasized the degree of resource partitioning by demersal fish. In general, he found a low degree of overlap in food utilization. In the case of commercial species, however (*Champsocephalus gunnari*, South Georgia icefish *Pseudochaenichthys georgianus*, and painted notie *Notiotheniops larseni*), there was a relatively high degree of overlap. This group consists mostly of predators on krill. At one South Georgia station, all fishes preyed on krill.

The present study reports on a quantitative examination of the trophic relationships within the demersal fish community on the continental shelf (~5 km offshore) around South Georgia I.

Methods

The specimens for this study were collected from the research vessel RV *Profesor Siedlecki* using commercial fishing gear, and represent the fishable community that was present during December 1987–January 1988. Fish were collected by 30-minute tows of a P32/36 otter trawl (mouth opening of 17.5 m, 43–52 mm mesh liner) as part of the 1987–88 Antarctic Marine Living Resources (AMLR) survey of the fish stocks around South Georgia I. Successful trawls were made at 108 stations within about 5 km of the island (Fig. 1). These stations were randomly located over the continental shelf within three depth strata (50–150 m, 150–250 m, 250–500 m) (Gabriel 1987, McKenna and Saila 1989). The collection methods are described in detail by McKenna and Saila (1989).

This sampling provided a substantial size range of individuals from the common species and at least a few representatives of most of the rare species (Table 1; McKenna 1990, app. C). A total of 321 stomachs were collected from 15 species of fish. Three of the fifteen species from which stomachs were collected belonged to the icefish family (Channichthyidae; *Champsocephalus gunnari*, black-finned icefish *Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*). Eight species were Antarctic cods (Nototheniidae; *Notothenia rossii*, gray rockcod *Notothenia squamifrons*, striped rockcod *Pagothenia hansoni*, *Notiotheniops larseni*, yellowfin notie *Notiotheniops nudifrons*, humped rockcod *Notothenia gibberifrons*, Patagonian rockcod *Patagonothen brevicauda guntheri*, and Patagonian toothfish *Dissostichus eleginoides*). Two species of Bathydraconidae (South Georgia icedragon *Parachaenichthys georgianus*, and bronze icedragon *Psilodraco breviceps*) were represented. The remaining two were members of some of the less-common families of the region (Artedidraconidae: fancy plunderfish *Artedidraco mirus*, Mureanolepididae: smalleye morey cod *Muraenolepis microps*.

Length (TL and SL) and weight measurements were taken for fish from each trawl. A stomach index value was also recorded for each fish. This index ranged from zero (empty stomachs) to five (full stomach). Individuals with a stomach index (Permitin and Tarverdieva 1979)

Table 1

Number of stomachs from each fish species collected at South Georgia I., used in diet analyses. n = number of stomachs which contained identifiable prey. Pooled n category = number of replicates used in the community-wide cluster analysis. # = number of stomachs used in the determination of numerical abundance of prey items.

		Number of stomachs					
		n			Pooled n		
Fish species	Species code	#	Wet wt.	Dry wt.	#	Dry wt.	Empty
Artedidraco mirus	ARTE	4	4	4	4	4	1
Chaenocephalus aceratus	ACER	19	19	19	7	7	16
Champsocephalus gunnari	GUNN	41	43	41	15	15	2
Dissostichus eleginoides	ELEG	50	50	50	18	18	0
Muraenolepis microps	MICR	6	6	6	2	2	0
Notothenia gibberifrons	GIBB	22	23	21	8	7	0
Notothenia rossii	ROSS	25	25	25	9	9	1
Notothenia squamifrons	SQUA	13	13	13	5	5	0
Nototheniops larseni	LARS	7	8	7	3	3	3
Nototheniops nudifrons	NUDI	12	14	12	4	4	0
Pagothenia hansoni	HANS	9	9	9	3	3	0
Parachaenichthys georgianus	PARA	9	9	9	3	3	0
Patagonothen brevicauda	GUNT	8	10	7	4	3	0
Pseudochaenichthys georgianus	PSEU	27	27	27	9	9	7
Psilodraco breviceps	PSIL	3	3	3	3	3	0

greater than zero were selected arbitrarily from the catch for gut content analysis. The sex of each fish was also noted. These data were recorded and the stomach was assigned an identification number for correlation with station information.

Stomachs were removed, taking care to prevent loss of any contents. Each stomach was preserved by injection with 10% formalin and wrapped in gauze or paper towels. Large stomachs were soaked in a 10% formalin solution for at least 24 hours. Stomachs were sealed in plastic ziplock bags and stored until they could be examined.

Examination of stomach contents

In the laboratory, the weights of all fish and stomach contents were measured to within 0.001 g on an electronic balance. Objects weighing more than 160 g were measured on a triple-beam balance. Before contents were removed from the stomach, the total formalin-preserved wet weight was measured. The stomach was then opened with a longitudinal incision through the stomach lining from esophagus to intestine. The contents were removed and sieved through a 0.5 mm mesh screen. Wet weight of the empty stomach lining was then measured. This allowed back-calculation of the wet weight of unidentifiable material (GORP) by the difference between total wet weight and the sum of the weights of the separate, identifiable items plus stomach lining. Empty stomachs and those containing only unidentifiable material were not used in the analysis of similarity.

Items remaining on the sieve screen were sorted into general taxonomic groups (e.g., fish, amphipod, isopod) and then identified to family or species where possible. Each group was enumerated and weighed. Specimens were then placed in a drying oven at 60°C and dried to constant weight.

Analysis of the diet data

Frequency of occurrence and dietary coefficients (Linkowski et al. 1983) were determined as simple measures of the importance of each potential prey item in the diet of each species (Table 2). To remove the biases due to varying stomach size and total number of items contained in each stomach, all diet data were converted to percent composition. Percent composition of the diet was determined for each stomach based on numerical abundance, wet weight, and dry weight of the prey items. Results refer to the use of percent composition by dry weight unless stated otherwise. Average percent composition of the diet was then calculated for each of the 15 species of fish for which stomachs had been collected (Table 3). Only stomachs which contained identifiable prey items were included in the diet analysis.

Table 2

Frequency of occurrence (%), dietary coefficient (Q), and diversity values for the diets of 15 Antarctic demersal fish species collected off South Georgia I. SPP = fish species code (see Table 1 for key to specific identification); %f = percent frequency of occurrence; Q = average number of prey × average dry weight of prey; H = Shannon-Wiener diversity index using average percent composition of the diet of each species; var(H) = variance of Shannon-Wiener index (Hutcheson 1970).

SPP:	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Fish															
%f	84.62	0.00	96.00	0.00	0.00	37.50	11.11	0.00	33.33	0.00	77.78	62.96	0.0	52.00	0.00
Q	6.92	0.00	7.65	0.00	0.00	0.48	0.00	0.00	0.09	0.00	1.91	6.65	0.0	7.27	0.00
Krill															
%f	15.38	25.00	18.00	50.00	100.00	100.00	100.00	42.86	16.67	83.33	22.22	59.26	100.0	76.00	30.77
Q	0.91	0.01	0.01	0.08	58.89	15.01	7.96	0.07	0.00	0.19	0.13	64.11	1.8	165.14	0.00
Tunicate															
%f	0.00	0.00	0.00	31.82	0.00	0.00	11.11	28.57	16.67	0.00	0.00	3.70	0.0	44.00	84.62
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.17	5.73
Amphipod															
%f	0.00	25.00	2.00	68.18	0.00	0.00	11.11	28.57	50.00	25.00	0.00	0.00	0.0	32.00	61.54
Q	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.02	0.01	0.02	0.00	0.00	0.0	5.12	0.01
Isopod															
%f	0.00	50.00	0.00	36.36	0.00	0.00	11.11	0.00	0.00	8.33	0.00	0.00	0.0	20.00	38.46
Q	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Polychaete															
%f	0.00	50.00	0.00	86.36	2.44	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	8.00	23.08
Q	0.00	0.00	0.00	6.56	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.0	0.03	0.01
Shrimp															
%f	15.38	0.00	6.00	9.09	0.00	0.00	0.00	0.00	16.67	0.00	66.67	0.00	0.0	28.00	0.00
Q	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.09	0.00	0.0	0.19	0.00
Echiura															
%f	0.00	0.00	0.00	22.73	0.00	0.00	0.00	0.00	16.67	8.33	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Gastropod															
%f	0.00	0.00	0.00	45.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	8.00	7.69
Q	0.00	0.00	0.00	36.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Rocks															
%f	0.00	0.00	4.00	13.64	0.00	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Diversity															
H	0.988	1.464	0.198	1.772	0.00	0.573	0.389	1.296	1.701	1.148	0.96	0.677	0.0	1.306	1.613
var(H)	0.0107	0.0018	0.0042	0.0143	0.00	0.0022	0.0092	0.0019	0.004	0.0086	0.0028	0.0004	0.0	0.0101	0.017

Similarity analysis was used to classify fish species into distinct trophic groups based on their diets. Two techniques were used. The first, based on the work of Smith (1985), generated a matrix of similarity coefficients and associated variances for each pair of species being compared. Similarity was measured with the proportional similarity coefficient (PS) for each pair of fish species being compared. This analysis was based on the average percent composition for each species.

The second method applied cluster analysis to these data. I used the clustering methods of Nemec and Brinkhurst (1988), which use a bootstrap technique applied to replicate samples to determine the significance of clusters. The Bray-Curtis similarity coefficient was used and, where replicates were available, significance was tested using 50 bootstrap simulations. For each species, a separate cluster analysis was performed to determine if there were significant intraspecific subgroups by size, sex, or depth of habitat (McKenna 1990, app. D). Although the variability in diet of each species was obvious, no significant subgroups were identified.

Cluster analysis was then applied to examine the structure of the community. There is virtually no spatial structure to the South Georgia fish community at this season (McKenna 1990:178–251) and, since no significant intraspecific structure was found, each stomach examined was used as a replicate sample of the diet of the predator species (Table 1). These data were used in the SIGTREE cluster analysis program (Nemec and Brinkhurst 1988). Due to a limitation of the program (a maximum of 110 observations [sum of replicates per species] are allowed), the data were pooled into groups of three and averaged to reduce the number of observations from 264 to 97 (Table 1).

Table 3

Average percentages of total diet contributed by each prey species for 15 Antarctic demersal fish species collected around South Georgia I. Asterisk (*) = prey item accounted for <0.1% of the diet. See Table 1 for key to species code identifications.

Prey item	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Based on numerical abundance of prey items															
Fish	59.6	0.0	83.6	0.0	0.0	15.5	2.8	0.0	13.9	0.0	39.1	43.9	0.0	14.2	*
Krill	18.5	15.0	11.1	5.2	99.3	84.5	86.1	33.3	4.2	65.3	22.2	56.1	100.0	64.6	5.6
Tunicate	0.0	0.0	0.0	5.1	0.0	0.0	5.6	16.7	8.3	0.0	0.0	*	0.0	9.5	47.5
Amphipod	0.0	16.7	*	10.9	0.0	0.0	2.8	38.9	20.8	10.1	0.0	0.0	0.0	3.6	32.8
Isopod	0.0	30.0	0.0	1.4	0.0	0.0	2.8	0.0	0.0	1.4	0.0	0.0	0.0	*	5.0
Polychaete	0.0	13.3	0.0	52.3	0.6	0.0	0.0	0.0	16.7	11.4	0.0	0.0	0.0	0.6	3.9
Shrimp	16.2	0.0	3.1	*	0.0	0.0	0.0	0.0	5.6	0.0	38.7	0.0	0.0	5.4	0.0
Echiura	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	*
Ctenophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Cumacid	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropod	0.0	0.0	0.0	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	1.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	1.7	*	0.0	0.0	0.0	0.0	13.9	3.5	0.0	0.0	0.0	0.0	2.2
Based on wet weight of prey items															
GORP	18.8	48.0	6.1	41.5	12.4	42.7	26.0	34.7	30.9	26.9	9.6	14.3	6.6	21.2	19.6
Fish	60.3	0.0	88.7	0.0	0.0	10.3	0.0	0.0	15.8	0.0	49.9	50.0	0.0	27.1	0.0
Krill	7.9	16.5	4.7	1.4	85.4	46.9	71.2	31.9	2.1	49.8	21.2	35.5	93.4	38.6	1.5
Tunicate	0.0	0.0	0.0	4.9	0.0	0.0	2.3	12.1	3.1	0.0	0.0	*	0.0	7.7	66.6
Amphipod	0.0	2.6	*	2.1	0.0	0.0	*	8.7	5.0	4.7	0.0	0.0	0.0	1.7	3.0
Isopod	0.0	27.3	0.0	*	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0	*	2.0
Polychaete	8.0	4.4	0.0	28.6	*	0.0	0.0	0.0	25.1	10.6	0.0	0.0	0.0	*	1.7
Shrimp	0.1	0.0	*	3.3	0.0	0.0	0.0	0.0	1.2	0.0	19.3	0.0	0.0	2.0	0.0
Echiura	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	15.5	6.9	0.0	0.0	0.0	0.0	4.2
Gastropod	0.0	0.0	0.0	12.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	*	0.0
Based on dry weight of prey items															
Fish	63.4	0.0	95.2	0.0	0.0	37.8	4.4	0.0	25.5	0.0	58.6	58.9	0.0	36.1	*
Krill	10.3	18.5	4.3	4.8	99.6	62.2	90.7	33.3	2.0	62.1	21.9	41.0	100.0	45.5	3.8
Tunicate	0.0	0.0	0.0	7.5	0.0	0.0	3.6	22.8	9.5	0.0	0.0	*	0.0	6.2	48.8
Amphipod	0.0	3.2	*	5.3	0.0	0.0	*	32.8	9.6	12.7	0.0	0.0	0.0	4.0	10.0
Isopod	0.0	30.2	0.0	1.5	0.0	0.0	1.2	0.0	0.0	*	0.0	0.0	0.0	*	9.0
Polychaete	0.0	23.1	0.0	48.4	*	0.0	0.0	0.0	31.1	12.2	0.0	0.0	0.0	*	2.2
Shrimp	17.5	0.0	*	4.5	0.0	0.0	0.0	0.0	5.6	0.0	19.1	0.0	0.0	3.2	0.0
Echiura	0.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	5.1
Gastropod	0.0	0.0	0.0	14.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	5.7
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	*	3.0	0.0	0.0	0.0	0.0	*	4.2	0.0	0.0	0.0	0.0	6.9
Other	5.0	0.0	1.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	8.0

Results

Krill and fish were the dominant items in the diets of these fish (Table 2). In addition to these items, 26 types of invertebrates and plant material were represented in the guts (Sponges, Ctenophores, Cnidarians, Nemeratines, Nematodes, Bivalves, Cephalopods, Picnogonids, Cumacids, Tanaids, Copepods, Mysids, Bryozoans, and Echinoderms accounted for less than 1% of the diet). Of the 321 stomachs examined, 26 were discarded because they were not properly preserved, 30 were empty, and 13 contained only unidentifiable material. The highest proportion of unidentifiable material (among the stomachs used in the similarity anaysis) was 48% (on a wet weight basis) and occurred in *Artedidraco mirus* (Table 3). The ratio of dry weight to wet weight of unidentifiable material averaged 22%. This is within the range of values for identifiable prey items in the diets and was most similar to the same ratio for fish (Table 4). Despite the problems of differential digestion, it was assumed that the proportions of identifiable material were accurate representations of the diet of these fish.

Every species examined ate some krill (Table 2). However, most pairwise comparisons of species diets

Table 4

Dry- to wet-weight ratios for the most common prey items in the diets of 15 species of Antarctic demersal fish.

Prey taxon	Identified species	Dry:Wet (%)
Amphipod	*Vibilia antarctica*	18.62
	Parathemisto gaudichaudii?	
	Hyperiidae	
	Hyperoche medusarum?	
Echirua		24.01
Fish	*Chaenocephalus aceratus*?	23.79
	Artedidraco mirus?	
	Dissosticus eleginoides	
	Champsocephalus gunnari	
	Patagonothen brevicauda?	
	Pagothenia hansoni	
	Nototheniops larseni	
	Muraenolepis microps	
	Nototheniops nudifrons?	
	Parachaenichthys georgianus	
	Trematomus spp.?	
Gastropod	*Atlantica* spp.?	12.66
Isopod	*Arcturus* spp.?	15.42
Krill	*Euphausia superba*	17.76
Polychaete	*Sternapsis* spp.?	17.58
	Maldanidae	
	Lumbrineridae?	
	Terribellidae?	
	Philodocidae?	
Shrimp	*Crangon antarcticus*?	18.42
Tunicate		9.76
GORP		22.06

showed less than 50% overlap (Tables 5, 6), suggesting that in most cases resource partitioning was occurring. This is supported by the cluster analysis which showed that there was more than one significant cluster (Figs. 2, 3). The species or groups of species distinguished by the cluster analysis were feeding on different sets of prey. There were three groups of species in the community: fish-eaters, krill-eaters, and benthic invertebrates feeders.

Fish-eaters

The four members of the fish-eating group included most of the large carnivorous species in the region. The diets of *C. aceratus* and *Parachaenichthys georgianus* showed the greatest similarity (Figs. 2, 3) within the fish-eating group and overlapped by 78% (Table 6). They fed predominantly on fish, but each species also consumed roughly similar proportions of krill *Euphausia superba* and shrimp *Notocrangon antarcticus* (Table 3). Although little is known about the life history of *Parachaenichthys georgianus*, both it and *C. aceratus* appear to be epibenthic in their behavior.

Chaenocephalus aceratus is the largest species of icefish found in the South Georgia region, growing up to 75 cm (Fischer and Hureau 1985). It is an ambush predator (Kock 1985b). Heavily calloused pelvic fins of older individuals indicate that it spends much of its time sitting on the bottom. Fish prey included *Parachaenichthys georgianus* and *N. larseni*, which were as much as 58% of its body size (TL).

Table 5

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the numerical abundance of prey items in each diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	—	0.2026	0.8118	0.0594	0.2043	0.2864	0.2321	0.2148	0.2362	0.2043	0.6687	0.6430	0.2043	0.4170	0.0614
ARTE	0.1773	—	0.1250	0.3013	0.1567	0.1500	0.2056	0.3167	0.3417	0.3785	0.1500	0.1500	0.1500	0.2420	0.3559
ELEG	0.3547	0.1094	—	0.0672	0.1200	0.2021	0.1528	0.1250	0.2372	0.1433	0.5440	0.5587	0.1200	0.3117	0.0847
GIBB	0.0559	0.2553	0.0633	—	0.0638	0.0571	0.1557	0.2089	0.4070	0.3248	0.0594	0.0573	0.0571	0.2101	0.3062
GUNN	0.1626	0.1342	0.1056	0.0605	—	0.9179	0.8611	0.4286	0.0484	0.6601	0.2222	0.5612	0.9922	0.5853	0.0681
GUNT	0.2379	0.1275	0.1810	0.0538	0.0754	—	0.8889	0.4286	0.1238	0.6534	0.3043	0.6433	0.9179	0.6607	0.0614
HANS	0.1896	0.1800	0.1364	0.1435	0.1196	0.0988	—	0.5120	0.1529	0.6951	0.2500	0.5892	0.8611	0.6970	0.1726
LARS	0.1687	0.2164	0.1094	0.1653	0.2449	0.2449	0.3213	—	0.3333	0.5296	0.2222	0.4288	0.4286	0.6104	0.4051
MICR	0.1804	0.2500	0.2014	0.3241	0.0466	0.1153	0.1388	0.2222	—	0.3743	0.2362	0.1808	0.0417	0.4043	0.3767
NUDI	0.1626	0.3038	0.1228	0.2696	0.2331	0.2265	0.2490	0.3357	0.2619	—	0.2222	0.5612	0.6534	0.6706	0.2510
PARA	0.4388	0.1275	0.3679	0.0559	0.1728	0.2482	0.1999	0.1728	0.1804	0.1728	—	0.6129	0.2222	0.4334	0.0614
PSEU	0.4088	0.1275	0.3518	0.0540	0.2463	0.3216	0.2733	0.2451	0.1482	0.2463	0.2373	—	0.5612	0.7148	0.0616
PSIL	0.1626	0.1275	0.1056	0.0538	0.0077	0.0754	0.1196	0.2449	0.0400	0.2265	0.1728	0.2463	—	0.5786	0.0614
ROSS	0.3300	0.2110	0.2631	0.1878	0.2505	0.3192	0.3415	0.3937	0.2950	0.2209	0.3394	0.3761	0.2438	—	0.2574
SQUA	0.0576	0.2923	0.0804	0.2484	0.0643	0.0576	0.1565	0.3205	0.2977	0.2193	0.0576	0.0578	0.0576	0.2152	—

Table 6

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the dry-weight abundance of prey items in each species diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	—	0.1665	0.7514	0.0924	0.1139	0.3723	0.1575	0.1145	0.3311	0.1139	0.7878	0.7033	0.1139	0.4819	0.0458
ARTE	0.1388	—	0.0460	0.3253	0.1862	0.1846	0.1980	0.2166	0.2827	0.3434	0.1846	0.1846	0.1846	0.2229	0.2043
ELEG	0.2576	0.0439	—	0.0514	0.0459	0.3043	0.0896	0.0460	0.2798	0.0468	0.6373	0.6353	0.0459	0.3833	0.0444
GIBB	0.0839	0.2522	0.0488	—	0.0491	0.0475	0.0966	0.1757	0.5578	0.3111	0.0930	0.0482	0.0475	0.1918	0.3132
GUNN	0.1009	0.1521	0.0438	0.0468	—	0.7416	0.9073	0.4286	0.0213	0.6224	0.2194	0.4099	0.9961	0.4929	0.0451
GUNT	0.2926	0.1505	0.2354	0.0452	0.1916	—	0.7852	0.4286	0.2751	0.6208	0.4778	0.6683	0.7416	0.7497	0.0435
HANS	0.1426	0.1637	0.0856	0.0919	0.0841	0.2333	—	0.4661	0.1008	0.6275	0.2630	0.4542	0.9073	0.5799	0.0926
LARS	0.1014	0.1697	0.0439	0.1448	0.2449	0.2449	0.2810	—	0.2107	0.5561	0.2194	0.4106	0.4286	0.5165	0.2948
MICR	0.2215	0.1231	0.2041	0.3968	0.0209	0.1994	0.0938	0.1663	—	0.3212	0.3311	0.2758	0.0197	0.4079	0.2566
NUDI	0.1009	0.2804	0.0446	0.2611	0.2370	0.2354	0.2360	0.3561	0.2656	—	0.2200	0.4099	0.6208	0.5270	0.2170
PARA	0.4035	0.1505	0.2904	0.0845	0.1713	0.3629	0.2130	0.1713	0.2215	0.1716	—	0.8056	0.2194	0.5872	0.0470
PSEU	0.3429	0.1505	0.2858	0.0459	0.2419	0.4335	0.2837	0.2420	0.2001	0.2419	0.1566	—	0.4099	0.7433	0.0442
PSIL	0.1009	0.1505	0.0438	0.0452	0.0039	0.1916	0.0841	0.2449	0.0193	0.2354	0.1713	0.2419	—	0.4913	0.0435
ROSS	0.3335	0.1874	0.2701	0.1687	0.2515	0.4416	0.3245	0.3251	0.3146	0.2544	0.4038	0.4640	0.2499	—	0.1531
SQUA	0.0437	0.1736	0.0425	0.2610	0.0432	0.0416	0.0883	0.2472	0.2233	0.1720	0.0451	0.0423	0.0416	0.1393	—

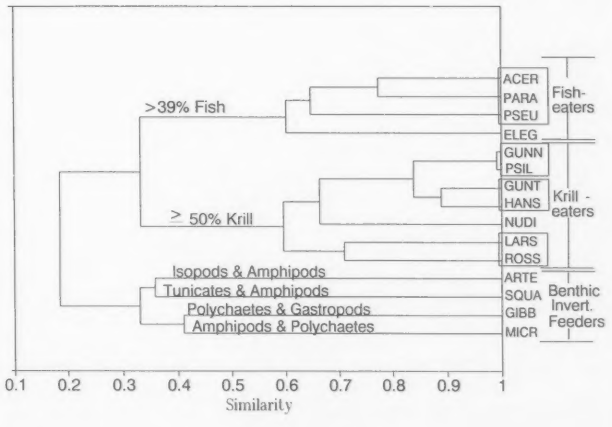

Figure 2

Dendrogram representing the classification of Antarctic demersal fish into trophic groups based on numerical abundance of prey items in their guts. Refer to Table 1 for key to species codes. Species grouped together within a box were identified as having significantly similar diets.

Parachaenichthys georgianus has a scaleless, elongate body. Its mouth is tube-shaped and probably functions like a slurp gun. It may be an ambush predator like the *C. aceratus*. Its diet consisted mainly of fish (59%) and roughly equal proportions of krill and shrimp (Table 3). None of the fish it consumed were identifiable. Its diet overlapped most (80%) with that of the *Pseudochaenichthys georgianus* (Table 6).

Pseudochaenichthys georgianus also preyed heavily on other fish (59%)(Table 3). Like *C. aceratus*, it has a large mouth. However, it tended to feed on smaller fish and more krill than *C. aceratus* and did not eat shrimp. It fed on a variety of other fish species including *N. larseni*, *C. gunnari*, *M. microps*, and *Parachaenichthys georgianus*. Its diet overlapped most (80%) with that of *Parachaenichthys georgianus*.

D. eleginoides is the largest of all Antarctic demersal fish, growing to over 2m, and is an active predator (Fischer and Hureau 1985). It is known to be pelagic during some stages of its life (Fischer and Hureau 1985), but the presence of rocks in a few stomachs indicates that some had been feeding close to the bottom. It fed almost exclusively on fish (97%) (Table 3). Based on identifiable fish in the guts, it preyed on *M. microps*, *N. larseni*, *Parachaenichthys georgianus*, and its own young. Stomachs from this species often contained a single fish that was as much as 53% of the size (TL) of the predator. Its diet overlapped most (75%) with that of *C. aceratus*.

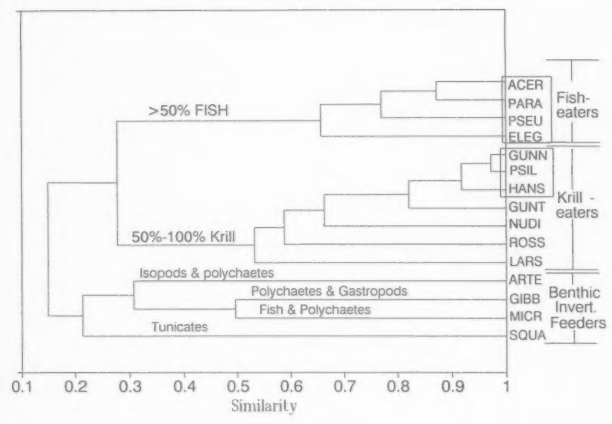

Figure 3

Dendrogram representing the classification of Antarctic demersal fish into trophic groups based on dry weight of their gut contents. Refer to Table 1 for key to species codes. Species grouped together within a box were identified as having significantly similar diets.

Krill-eaters

Seven species were grouped as krill-eaters. The hierarchical cluster analysis places *C. gunnari*, *P. breviceps*, and *P. hansoni* in a single cluster and identifies others within this group as distinct clusters. The cluster analysis arranged these species in order of decreasing proportion of krill in the diet (Fig. 3, from top to bottom). These species are probably more pelagic in nature than other members of the community, with the possible exception of *N. nudifrons* (Permitin and Tarverdiyeva 1972, Targett 1981).

C. gunnari and *P. breviceps* had the most similar diets (Table 6), feeding almost exclusively (>97%) on krill. *Psilodraco breviceps* diet consisted 100% of krill (Table 3), but only three specimens were examined and the true variability of this species' diet may not be accurately represented here.

Champsocephalus gunnari is the most important commercial species around South Georgia (Kock 1986, Gabriel 1987, McKenna and Saila 1989). It leads a more pelagic existence than its local relatives (*C. aceratus*, *P. georgianus*) (Kock 1985b). Its heavy dependence on krill has been documented (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979, Tarverdiyeva and Pinskaya 1980, Kock 1981). In this sample, its diet was composed almost entirely (99%) of krill (Table 3).

Little is known about the life history of *P. hansoni*, except for its heavy dependence on krill (Targett 1981). In 1987–88, its diet consisted primarily of krill (91%), but it also fed on fish and tunicates (Table 3). Its diet overlapped those of *C. gunnari* and *P. breviceps* by more than 90% (Table 6).

Patogonothen brevicauda is endemic to a shallow shelf region west of South Georgia known as Shag Rocks. Its diet consisted of 80% krill and 20% fish (Table 3). Its diet overlapped that of four other species (*C. gunnari*, *P. hansoni*, *P. breviceps*, and *N. rossii*) by more than 70%, due to the heavy dependence on krill (Table 6).

Nototheniops nudifrons is thought to be benthic in nature (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979). However, in 1987–88, 66% of its diet consisted of krill (Table 3) and the remainder was composed of epibenthic invertebrates. Rocks accounted for about 0.5% of the average dry-weight contents. Its diet overlapped that of four other species (*C. gunnari*, *P. brevicauda*, *P. hansoni*, and *P. breviceps*) by 62% (Table 6).

Notothenia rossii is a large (90 cm) species that was the mainstay of the commercial catch during the early 1970s (Kock 1986). Its diet was diverse, but it was grouped with the krill-eaters because 46% of its food was krill (Table 3). Fish was the second-most-important item in its diet and included *Parachaenichthys georgianus*, *M. microps*, *P. hansoni*, and *N. larseni*. *Notothenia rossii*'s diet overlapped most (74%) with those of *Pseudochaenichthys georgianus* and *P. brevicauda* (Table 6).

Nototheniops larseni is considered to be one of the most pelagically adapted of the nototheniids (Targett 1981). Previous work has shown that its diet is often dominated by krill (Permitin and Tarverdyieva 1972 and 1979, Targett 1981, Daniels 1982). In this study, krill comprised only one-third of its diet, and 56% was pelagic tunicates and amphipods (Table 3). Its diet overlapped that of *N. nudifrons* by 55% (Table 6).

Consumers of benthic invertebrates

All of the members of the 'benthic invertebrate feeders' group had diets which were distinct from one another as well as from members of the other major groups. However, these fish all seemed to be closely associated with the bottom.

Notothenia squamifrons diet was the most unusual of all the species examined. It included a large proportion (49%) of tunicates (salps) (Table 3). The remainder of its diet consisted almost entirely of benthic invertebrates. Krill made up only 4%. The preponderance

of salps is also a feature of the diet of *N. squamifrons* found at Kerguelen I. (Duhamel and Hureau 1985). *Notothenia squamifrons* diet displayed the least amount of overlap of all the species examined. It reached a maximum of 32% when compared with that of *N. gibberifrons* (Table 6).

Polychaetes were a major component (>23%) of the diets of the three remaining species. *Notothenia gibberifrons* is an important commercial species. It was the dominant species (numerically and by biomass) during the 1988–89 AMLR survey of the South Georgia region (McKenna 1989). It is a benthic species, which uses its relatively small, subterminal mouth to 'slurp up' benthic epi- and infauna (Daniels 1982). It had the most diverse diet of the species examined (Table 2); however, over 50% of its diet consisted of polychaetes. The remainder was comprised of invertebrate epifauna and a small amount of krill (5%, Table 3). Its diet overlapped most (56%) with that of *M. microps* (Table 6).

Mureanolepis microps is a scaleless, eel-like species with a diverse diet (Table 2). It was the only 'benthic invertebrate feeder' to eat fish (Table 3). Nine percent of its diet consisted of salps and 2% of krill. The other items in the diet were benthic organisms. Polychaetes were the dominant prey item. Its diet overlapped most (56%) with that of the *N. gibberifrons* (Table 6).

Artedidraco mirus was the smallest species (~8 cm TL) consistently caught in the trawl. Its diet was composed mostly of isopods and polychaetes (Table 3). This species was represented by only four stomachs, which may not accurately display the true diet of this species at South Georgia. The greatest overlap of its diet (34%) occurred with *N. nudifrons* (Table 6).

Discussion

These results support the conclusions of earlier workers, in that the most abundant species (including those of commercial value) of the South Georgia demersal fish community can be classified into three groups based on their summer diets. The largest group contained those fish that depended heavily on krill and included *C. gunnari* and *N. rossii*. Fish-eaters represented a second distinct group. Three of the four members of this group (*D. eleginoides*, *C. aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The third group contained a loose association of species which tended to feed mostly on benthic invertebrates. *Notothenia gibberifrons* and *N. squamifrons* are the commercially important members of this group. *Notothenia gibberifrons* is one of the most abundant species in the region, while *N. squamifrons* is rare on the continental shelf around South Georgia (<500 m) (McKenna and Saila 1989, McKenna 1989).

The fishes at South Georgia were using two different food resources: pelagic organisms (mostly krill) and benthic organisms. The large benthic biomass of the Antarctic appears incapable of supporting a large or diverse fish fauna because most of it is in the form of non-food species (e.g., sponges, sea stars) (Belyaev and Ushakov 1957, Andriashev 1965). This may explain why *N. gibberifrons*, and a few less-common species, were the only fish that depended heavily on benthic organisms. To survive in this environment, these fish have had to diversify their diets and draw upon more prey species than the pelagic fish of the region.

The majority of fish in the vicinity of South Georgia I. relied on the pelagic food resource. The adaptations of many of these basically benthic fishes to pelagic feeding (Nybelin 1947, Permitin 1970, Eastman 1985, Kock 1985b) indicate the relative superiority, in quality and/or availability, of food in the pelagic realm. Krill was the only food resource consumed by all species of Antarctic fish examined in this study. Five of the fifteen species examined relied on krill for greater than 50% of their diet.

There were direct and indirect trophic links between krill and piscivores. All piscivores ate some krill, and most of the identifiable fish that they ate were krill-eaters. However, most of the fish consumed by piscivores in this study were unidentifiable, and a stong link between a piscivore (*N. rossii*) and the benthos (*N. gibberifrons*) has been demonstrated at Kerguelen I. (Linkowski et al. 1983). Thus, the relative magnitudes of links between piscivores and krill or the benthos remain unknown.

Diet overlap and interspecific competition

In paired comparisons, there was at least some overlap in the diets, especially in those species relying heavily on krill. However, in most cases the overlap was less than 50%, indicating that resources were effectively partitioned within the South Georgia community during the austral summer.

Despite the heavy dependence on krill and high overlap (90%) of the diets of a few species, competition is probably not important in the Antarctic demersal fish community during the summer (Targett 1981, Daniels 1982). Competition occurs only when the resource in common use is limiting (Larkin 1963). The availability of krill to Antarctic fish varies (Permitin and Tarverdieva 1979), but whether it is limiting is unknown. In some years, krill is abundant enough to come in contact with the bottom and is then available to even strict benthic feeders like *N. gibberifrons* (Targett 1981).

This study suggests that resources are effectively partitioned in the austral summer. However, the Antarctic undergoes strong seasonal changes, which affect the abundance and availability of krill as well as other aspects of the ecosystem. Krill spawn in summer and the larvae migrate vertically from great depths (>500 m) as they develop over the winter, recruiting to the population the next summer (Marshall 1979). Adult and juvenile krill do most of their growing in summer when they may be superabundant, occurring in dense 'swarms' (Everson 1984a). During the unproductive winter, krill grow little or may even shrink in size (Ikeda and Dixon 1982), but their distribution at that time is poorly known.

The trophic structure of the Antarctic fish community may change in response to these seasonal events. Prey switching and niche shifts offer two mechanisms to deal with these seasonal changes. Although diet diversities were low for South Georgia fishes, all species (with the exception of *P. breviceps*) consumed at least one alternative food resource regularly. This indicates that there is the potential for prey switching according to the availability of the prey resources in the environment. Seasonal prey switching has been inferred from changes in the diets of related species living along the Antarctic Peninsula (Daniels 1982).

Niche shifts may occur to reduce competition at times when krill is limiting. As krill becomes more limiting, behaviorial changes, such as a shift to more specialized feeding on alternative prey or in specific habitats, may occur. To test these hypotheses a seasonal time series of diets and the availability of prey is needed.

Possible effects of commercial fishing

Selective removal of species by fishing will effect the demersal fish community. Prey of removed predators may benefit from reduced predation, as has been suggested for *Champsocephalus gunnari* at Kerguelen I. (Duhamel and Hureau 1985). One competitor may benefit by increased fecundity if the other is removed by fishing (Beddington and May 1982). Competition may be intensified at a lower trophic level if a predator on one species of a competing pair is reduced (Miller and Kerfoot 1987, Abrams 1987, Boisclair and Leggett 1989). If a niche shift had taken place in the past to reduce competition, a species may expand to occupy more of a niche when its competitor is removed (Connell 1980, Beddington and May 1982). However, it is difficult to predict the response of the community without more data on the life histories and seasonal dynamics of these fish and their prey.

Ecological efficiency is another topic to be considered when harvesting an Antarctic community. The South Georgia community is highly productive (Hempel 1985). The diversity of the system is low and the food web is relatively simple (Beddington and May 1982). However, the cost of activity and survival in the Antarctic is high (Hempel 1985) and the loss of energy at each trophic transfer places a limitation on the biomass of fish available for harvest. Many of the commercially valuable species are large piscivores (*Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*, *Dissostichus eleginoides*, *Notothenia rossii*) one or more steps removed from secondary production. The availability of krill to these fish and their prey, and the fish's ability to emphasize krill in their diets, will strongly influence the yield of fish from the South Georgian community.

Conclusions

The most abundant species of the South Georgia demersal fish community were classified into three groups based on their summer diets. Species that depended heavily on krill comprised the largest group, including *Champsocephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consists of krill. The third group contained a loose association of species which fed mainly on benthic organisms. *Notothenia gibberifrons* and *Notothenia squamifrons* are the important commercial species in this group.

Krill is the most important prey species to the fish in the South Georgia system during the austrial summer. It was consumed either directly or indirectly by all of the fish in this study. However, it is unknown whether the krill resource is limiting to these fish at that time or in any other season. More information on the seasonal dynamics and behavior of these fish and their prey is necessary to conclusively determine the role of competition for food in this system.

The potential for change in this community due to fishing is evident. Selective reduction in populations within the fish community may have widespread repercussions. The relatively simple, but highly interconnected, food web in the South Georgia system may have a lower potential for fish yield than previously thought (Hemple 1985).

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Abstract. – The school shark *Galeorhinus galeus* was sampled by otter trawl on the continental shelf of southern Brazil from 1980 to 1986 between latitudes 32°S and 34°40′S, at depths between 10 and 500 m. The species is a winter migrant, present in the study area from April to November. A total of 1548 specimens were examined. Sexual maturity occurred at total length of 107–117 cm in males, and 118–128 cm in females. The reproductive cycle was annual in the male and three years in the female, with uterine rest and slow vitellogenesis during the first year, maturation of oocytes and copulation during the second year, and gestation during the third year. In November, the diameter of mature follicle was 4.6–5.5 cm, ovulation occurred, and full-term embryos occurred with average total length of 30.3 cm. Uterine fecundity varied between 4 and 41 with a mean of 23.1, of which 94.2% were normal embryos, 5.2% were non-developing eggs, and 0.6% were abnormal embryos. Copulation took place up to 5 months before ovulation, with passive transport of spermatophores through the uterus. Liver weight as a percent of gutted body weight averaged 8% in immature animals of both sexes, 7% in gravid females, 11% in adult males and nongravid females in the first year of the reproductive cycle, and 17% in non-gravid females in the second year of the cycle, and it decreased during winter.

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Sexual Development, Reproductive Cycle, and Fecundity of the School Shark *Galeorhinus galeus* off Southern Brazil

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Annual landings of demersal sharks at the port of Rio Grande, Brazil, increased from 1414 tons in 1973 to 3217 tons in 1986 and then decreased to 2023 tons in 1989 (SUDEPE 1990). This raises the question of the impact of increasing fishing effort on the stocks. The school shark *Galeorhinus galeus* comprises the major part of the landings (Wahrlich and Peres 1990). Accounts of fisheries for this species in other areas are classic examples of the rule that sharks are unable to maintain their abundance under heavy fishing. This is due to their live-bearing mode of reproduction, which implies that fecundity is low and recruitment is proportional to the abundance of the adults (Holden 1977). Management of the fishery requires estimates of reproductive parameters.

The reproductive cycle of female *G. galeus* has been described as annual off California and Tunisia, and biannual off Australia (Ripley 1946, Olsen 1984, Capapé and Mellinger 1988). However, the simultaneous occurrence of three distinct reproductive stages of adult females off southern Brazil led to the hypothesis of a triannual reproductive cycle (Vooren and Guzenski 1982). This hypothesis was tested in the present study.

This paper describes sexual maturation and the reproductive cycle for both sexes, and uterine and ovarian fecundity of female school shark off southern Brazil.

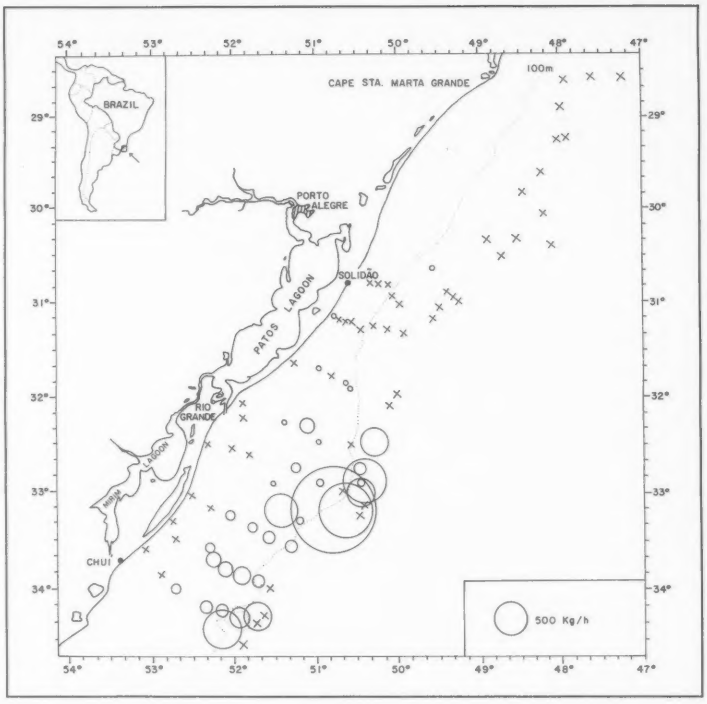
Materials and methods

The study area was the continental shelf of Rio Grande do Sul, between Cape Santa Marta Grande (lat. 28°40′S) and Chuí (lat. 33°44′S), Brazil. From June 1980 to September 1986, the area was surveyed during 12 cruises by the RV *Atlântico Sul*, at depths between 10 and 500 m, using an otter trawl with groundrope of 50 m and codend mesh of 45 mm between opposed knots (see Fig. 1 for location of stations). Tows lasted 60 minutes, and towing speed was 5.5 km/hour. Samples were also obtained with similar nets during five commercial trawling trips. The data series includes all months of the year except December and March. One specimen found on 13 December 1985 on the beach near Rio Grande, and nine specimens obtained on 24 June 1986 from commercial landings at Montevideo, were also examined.

In each haul, the weight of the catch (in g) and the body length (in cm) and sex of all specimens were recorded. Total length (TL) was measured with the tail aligned with the long axis of the body. Biological data were taken from random samples of the catches, totaling 904 females of 43.0–154.5 cm TL and 644 males of 43.5–148.0 cm TL. Weights (in g) of the whole body, liver, and gonads were recorded. Total body weight was measured until November 1983. Thereafter, the eviscerated body

Figure 1

The study area with sampling grid for the school shark *Galeorhinus galeus*, during 9–30 August 1983 (depths < 100 m) and 17 July–17 September 1986 (depths of 100–500 m) off Brazil. Surface area of circles indicates catch rates in kg/hour bottom trawling, and crosses indicate zero catches.



weight was measured, as recommended by Mellinger (1966), for study of certain aspects of reproduction. The gonad weight included that of the epigonal organ cut in front of the rectal gland. Epigonal organ weights were also measured in 43 specimens. In males, the length of the clasper was measured from the posterior origin of the pelvic fin. For females, the following data were recorded: diameter and color of the largest ovarian follicle, width of the nidamentary gland, presence or absence of embryos and uterine eggs, weight of the full gravid uterus, and greatest width of the nongravid uterus. Embryos were measured, sexed, and weighed with and without the yolksac. Fecundity was determined by counting maturing ovarian follicles ("ovarian fecundity") and uterine eggs and embryos ("uterine fecundity"). Hepatosomatic and gonadosomatic indices were calculated, using the weight of the organs as a percent of the eviscerated body weight. The latter indices were obtained using the linear regression equation of eviscerated weight as a function of total length. Separate equations were used for sexually immature sharks of both sexes, adult males, and adult females (Table 1).

Table 1

Biometric variables (Y) as a function of total body length (TL) in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. TL* indicates body length of the mother, N indicates sample size, R is correlation coefficient. Weights in g, lengths in cm.

Variable	Equation	N	R
Eviscerated weight, adult male	$Y = 3.95 \times 10^{-3} \times TL^{2.97}$	124	0.91
Eviscerated weight, adult female	$Y = 5.38 \times 10^{-4} \times TL^{3.39}$	128	0.93
Eviscerated weight, immatures	$Y = 2.15 \times 10^{-3} \times TL^{3.10}$	138	0.99
Weight of testis	$Y = -5.20\,TL^{3.32}$	131	0.74
Weight of epigonal organ, male	$Y = -4.67\,TL^{2.89}$	13	0.94
Ovarian fecundity	$Y = 0.49\,TL - 43.15$	57	0.68
Uterine fecundity	$Y = 0.53\,TL - 49.44$	137	0.66
Mean length of embryo per litter, June–July	$Y = 0.025\,TL^* + 18.78$	39	0.13
Mean length of embryo per litter, Aug–Sep	$Y = 0.14\,TL^* + 7.24$	46	0.44

Histological smears of the reproductive organs were obtained from 7 males and 17 females, ranging from 124 to 148 cm TL. Testes smears were made from cross-section surfaces on glass slides. The nidamentary gland was opened lengthwise and smears were made of the surface of its lumen on glass slides. Smears were also made of the contents of the epididymis and the seminal vesicle. Smears were fixed in a solution of equal proportions of ethanol and ethyl ether and stained with haematoxylin-eosin.

The present study follows Compagno (1988) with respect to nomenclature.

Results

Spatial and temporal distribution

School sharks were seasonally abundant at depths of 40–350 m, between latitudes 32°S and 34°30′S. In this area, mean catch rates per cruise were high from June to September, attaining values up to 376 kg/hour at depths between 40 and 100 m, and 620 kg/hour between 100 and 350 m. Figure 1 shows the sampling grid and catches for August 1983 and 17 July–17 September 1986. Within the study area, the entire area of distribution was covered by the sampling grid.

The species was scarce in April, May, October, and November, and absent in January and February. The school shark is characterized as a seasonal migrant, entering the study area in autumn, attaining peak abundance during winter, and leaving in spring.

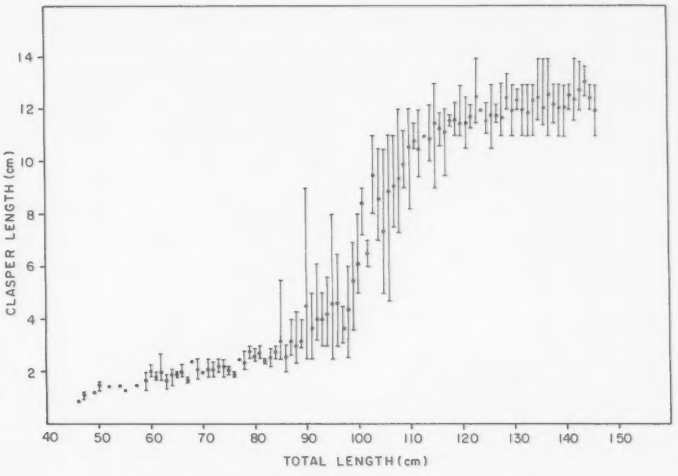


Figure 2

Relationship between total body length and length of clasper in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. Points indicate the mean, and vertical lines the range for length-class intervals of 1 cm.

Sexual development and organization of gametes in the male

Sexual maturation of the male was inferred from the length of the clasper. The relationship between clasper length and total length was sigmoid (Fig. 2). The curve rose steeply between 85 and 117 cm TL, and dispersion was greatest in this range. The curve flattened out for clasper lengths greater than 10.5 cm. This latter value was taken as the lower limit for sexual maturity. On the basis of this criterion, sexual maturation began at 85 cm TL. The smallest mature male measured was 107 cm TL, 50% maturity occurred at 111 cm, and all males greater than 117 cm were mature. The clasper of the adult measured, on average, 12.0 cm, ranging from 10.5 to 14.0 cm.

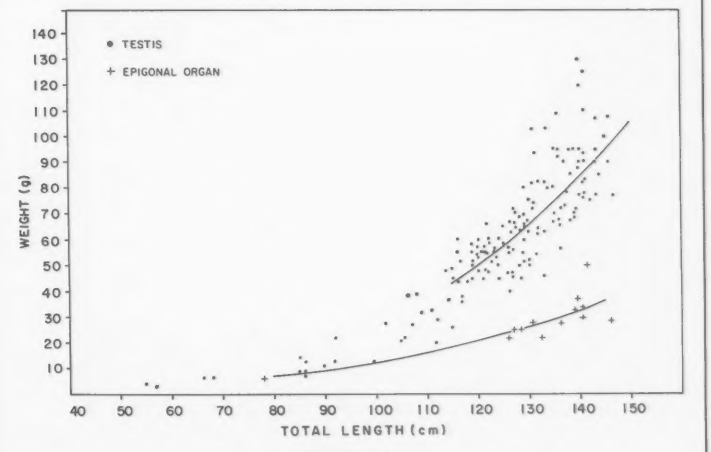


Figure 3

Relationship between total body length and weight of epigonal organs and testis in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Potential equations described adequately the relationship of gonad and epigonal organ weight to total length (Fig. 3, Table 1). At total lengths less than 85 cm, gonad weight was similar to the weight of the epigonal organ, and testes were not visually evident. Between 85 and 140 cm TL, epigonal organ increased from 10 to 30 g, and gonad weight increased to an

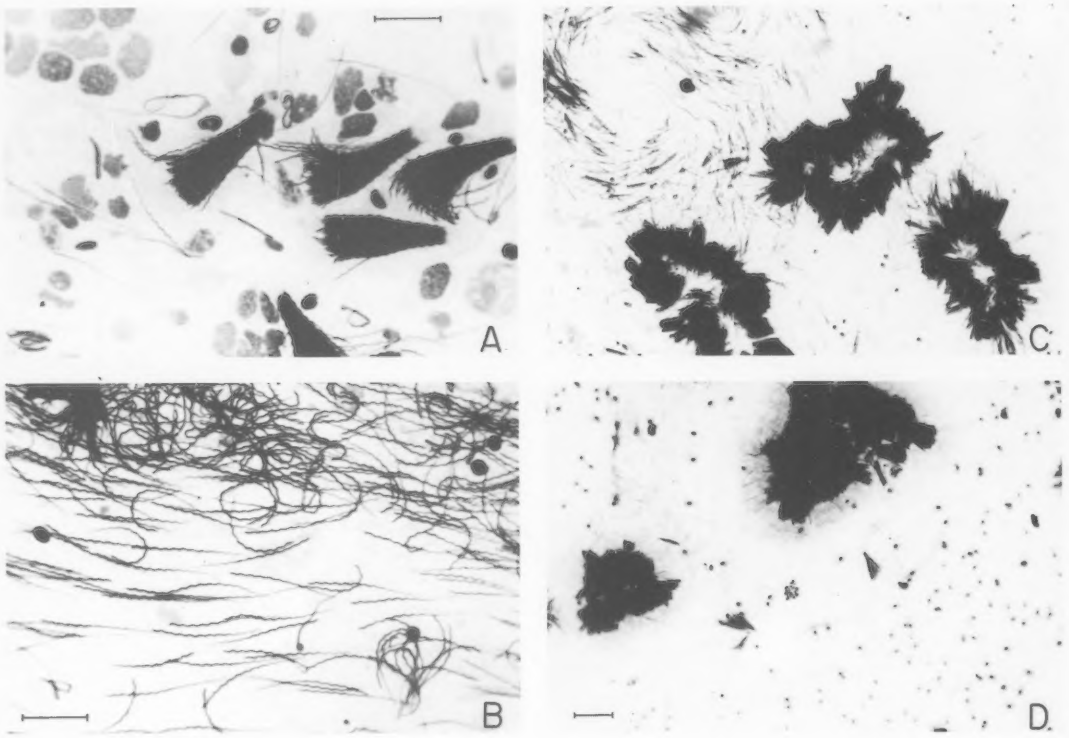


Figure 4

Spermatozoa in smears of reproductive organs of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. (A) testis, (B) epididymis, (C) seminal vesicle, (D) nidamentary gland of an adult nongravid female with mature ovary. Scale bars represent 20 μm.

average of 90 g. Thus, the increase of gonad weight with body size reflects mostly growth of the testes, and can be interpreted in terms of sexual development. The gonadosomatic index varied about the mean of 0.6 at total lengths less than 117 cm, and 0.9 at greater body lengths. The attainment of sexual maturity, as indicated by the clasper, was accompanied by a marked increase in relative weight of the testes. Growth of the testes continued after the attainment of sexual maturity, as indicated by gonad weights of 35–60 g at 115 cm TL, and 75–130 g at 145 cm TL.

Smears of the testes showed that sperm occurred in bundles within the testicular ampullae (Fig. 4A). In the epididymis, sperm occurred singly (Fig. 4B). The head of the spermatozoon measured, on average, 47 μm and the tail about 100 μm (n 62). In all smears of the seminal vesicle, sperm occurred in circular or oblong agglomerations, with their heads towards the center (Fig. 4C). Such structures were called spermatophores. The shortest and longest axes of the spermatophores measured, on average, 142 and 201 μm, respectively (n 64).

Sexual development of the female

The female has one functional ovary, situated on the right. Ovarian follicles were visible to the naked eye at total lengths greater than 80 cm. Follicle color varied with its diameter: transparent and colorless, up to 0.6 cm; opaque white, 0.4–1.2 cm; pale to sulphur yellow, 1.0–2.5 cm; and golden yellow, 3.5–5.5 cm. Follicles of ovulating females ranged from 4.6 to 5.5 cm, which is therefore the size range of the mature follicle. The weight of 58 mature ovaries increased with body size

and varied from 400 to 1600g, including the epigonal organ of 25–60g. Maturing ovaries contained 12 to 34 follicles of uniform size, with diameter greater than 3.5cm. Such ovaries occurred in females larger than 122cm TL (Fig. 5).

The smallest pregnant female was 118cm TL. Incidence of pregnancy increased to about 50% at body sizes greater than 130cm (Table 2). The developing uterus appeared as a strip of white tissue with diameters up to 0.3cm in females of less than 110cm. The uterus widened first at its posterior end, becoming bottle-shaped at lengths of 110–125cm TL, with a diameter of 1.0–2.3cm at its widest part. Fully-formed uteri, uniform in width, measured 2.0–4.0cm in diameter and occurred in females larger than 121cm TL. All nongravid females with total lengths greater than 128cm possessed such uteri.

The width of the nidamentary gland varied about 0.4cm in females of less than 112cm, and increased to values between 1.8 and 4.6cm in females larger than 125cm TL (Fig. 6).

Based on color and size of the ovarian follicle, width of the nidamentary gland and uterus, and the incidence of pregnancy, it is concluded that sexual maturity first occurred at 118cm TL, 50% maturity at 123cm TL, and full maturity at 128 cm TL. In the nongravid adult female, the uterus had a diameter of 2.0–4.0cm, the nidamentary gland was 1.8–3.5cm in width, and the ovary contained yellow follicles of diameters 1.4–5.5cm.

In one nongravid female of 154.5cm TL, the ovary was reduced to four atretic follicles with diameters less than 0.4cm, and the nidamentary glands were reduced in width (Fig. 6). The dorsal coloration of the body of this female was light grey with dark blotches. This 41-year-old female (Ferreira and Vooren 1991) was considered senile, the only such specimen encountered.

Reproductive cycle of the female

If the reproductive cycle of the female is synchronous at the population level, fertilization and birth should occur at definite seasons, and at any given time all gravid females should contain embryos in the same stage of development. If, in addition, the reproductive cycle lasts three years, three distinct categories of adult females are expected to simultaneously exist. A time-series of measurements of embryos and ovarian follicles, histological smears of the nidamentary gland, and seasonal records of ovulation showed that this was the case.

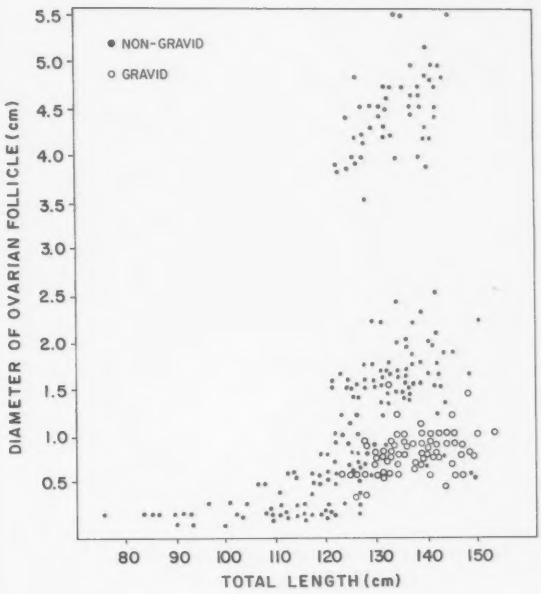


Figure 5

Relationship between total body length and diameter of the largest follicle in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Table 2

Incidence of pregnancy in *Galeorhinus galeus* from Rio Grande do Sul, Brazil, as a percent of the sample (n), by classes of total length (TL) in cm.

TL	% pregnant	n	TL	% pregnant	n
115	0	5	135	52	21
116	0	3	136	50	14
117	0	7	137	50	16
118	13	8	138	46	22
119	0	8	139	73	26
120	11	9	140	75	16
121	0	7	141	62	21
122	0	9	142	50	18
123	13	16	143	50	14
124	10	10	144	57	14
125	36	11	145	75	8
126	14	22	146	100	8
127	32	19	147	100	3
128	42	19	148	67	3
129	30	20	149	71	7
130	42	12	150	0	1
131	56	25	151	100	2
132	50	12	152	100	1
133	38	16	153	0	2
134	62	21	154	50	2

Within the study area, gravid females occurred from April to December and nongravid adult females from June to November. Ovulating females, females which had recently commpleted ovulation, and the largest mature ovarian follicles occurred in November and December. Full-term embryos without the yolksac were observed in November, as was also noted by De Buen (1952) off Uruguay. The monthly-length frequency distributions of embryos were unimodal, and modal embryonic total length increased from 13cm in April to 31cm in November (Fig. 7). Ovulation and birth both occurred in November–December, therefore gestation lasts 12 months.

In gravid females (GR), ovarian follicles were opaque white and did not grow (Fig. 8). Two distinct types of nongravid females occurred during the same time-periods each year. First-year nongravid females (NGR-1) occurred from June to September and had light-yellow ovarian follicles 0.5–2.5cm in diameter. Second-year nongravid females (NGR-2) were present July to November and had golden-yellow follicles of 3.5–5.5cm diameter.

From June to September, follicle diameter of NGR-1 females remained about 1.5cm (Fig. 9), while ovary weights ranged from 70 to 130g. Thus, vitellogenesis was slow. Females over the full size range of adults were classified as NGR-1 (Fig. 5). This category included the maturing, virgin phase but consisted mainly of resting females.

In NGR-2 females, the modal diameter of the largest follicle increased from 4.2cm in July to 5.5cm in November (Fig. 9). Accelerated vitellogenesis and ovarian maturation occurred in this phase. In November, these females had dilated nidamentary glands (the four greatest values in Fig. 6) and uteri containing a transparent viscous material resembling egg white.

The reproductive cycle of the female lasts three years. During the first 12 months after parturition, the oviduct remains in a resting stage and vitellogenesis is slow (NGR-1 stage). During the following 12 months, large mature follicles are produced, and the nidamentary gland and uteri are prepared for ovulation, which occurs in November–December (NGR-2 stage). Gestation lasts 12 months, during which there is no vitellogenesis, and parturition takes place in November–December (GR stage).

Nidamentary gland smears from one of eight NGR-2 females, collected in July 1986, had a large number of whole spermatophores, similar to those observed in the seminal vesicle of the male (Fig. 4). Thus, mating apparently begins during the NGR-2 phase as early as July, at least five months before ovulation, and the sperm is carried to the nidamentary gland by passive transport.

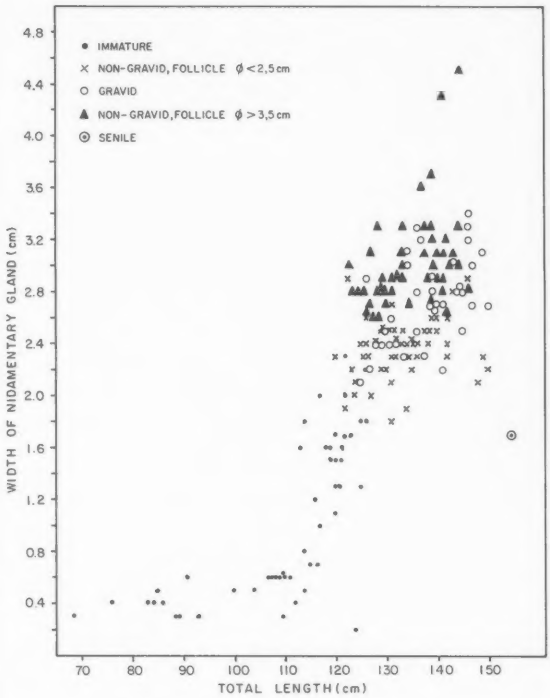


Figure 6

Relationship between total body length and width of the nidamentary gland in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Fecundity

Fecundity increased linearly with body size of the female (Table 1, Fig. 10). In 58 NGR-2 females of 123–146cm TL, ovarian fecundity ranged from 12 to 34 with a mean of 22.7 per female. In 140 females of 123–154cm TL, uterine fecundity ranged from 4 to 41 with a mean of 23.1. Of the items in the uteri, 94.2% were normal embryos, 5.2% were nondeveloping eggs, and 0.6% were dead or abnormal embryos. In 79% of the gravid females, there were at least one or two nondeveloping eggs, but the total number of these eggs per female, ranged up to 34.

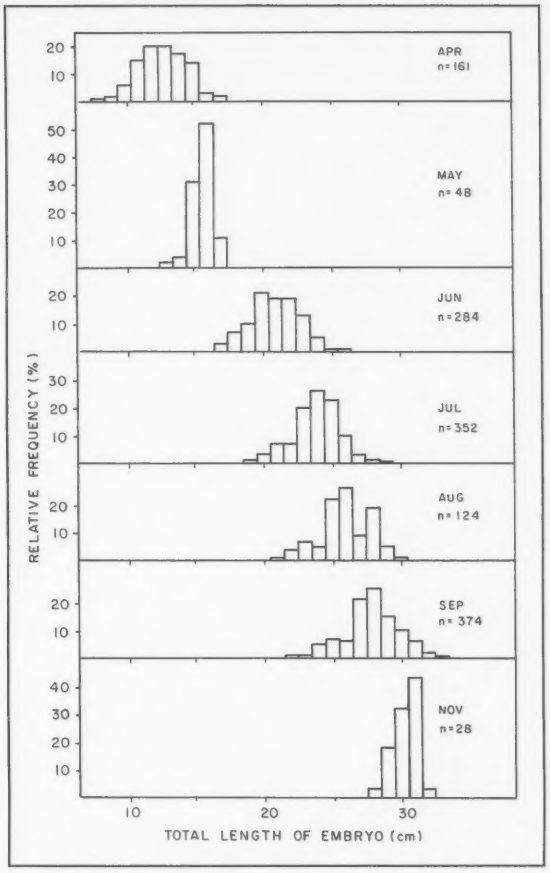


Figure 7 (above)
Monthly distributions of relative frequencies of total length of embryos of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

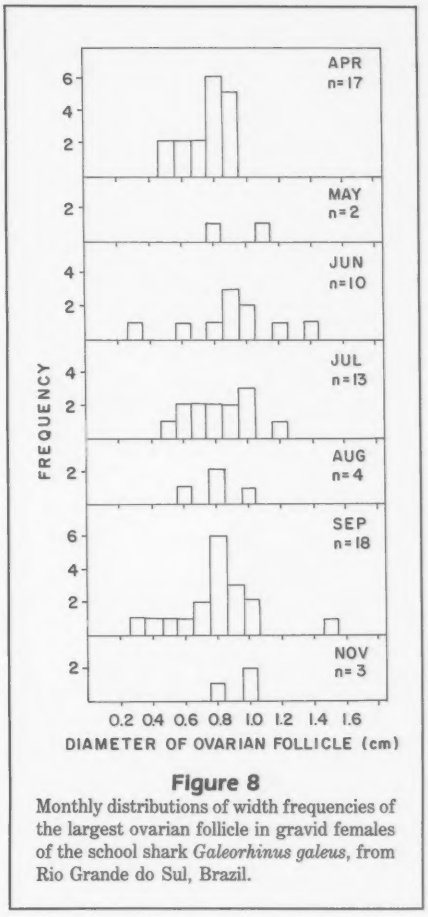


Figure 8
Monthly distributions of width frequencies of the largest ovarian follicle in gravid females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

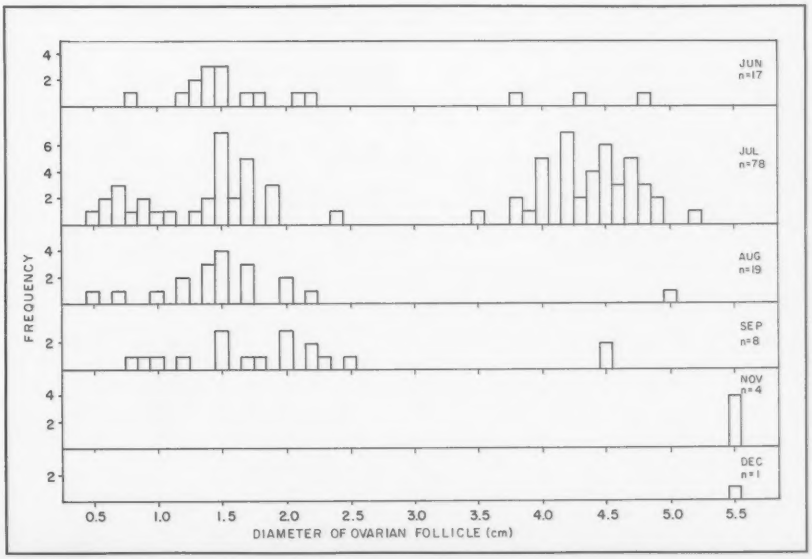


Figure 9 (right)
Monthly distributions of width frequencies of the largest ovarian follicle in nongravid adult females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

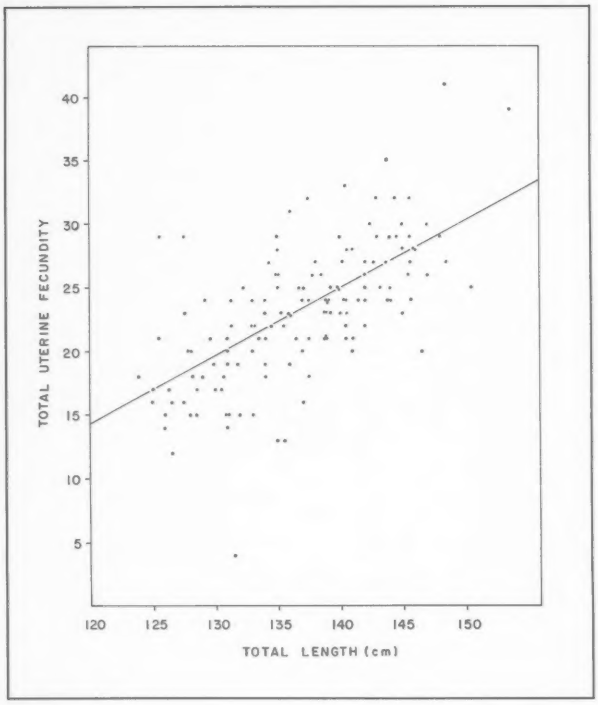


Figure 10
Relationship between total body length and uterine fecundity in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Gestation

Outgrowths of the uterine wall divided the uterus into separate gestation chambers for each embryo. The quantity of liquid in the chambers of the two uteri increased from about 200 g in April to 500–900 g in July, constituting respectively 8.3 and 28.0% of the weight of the full uteri in those months. Uteri were swollen and turgid due to the increasing mass of the litter and liquid, and in July attained weights between 1230 and 5520 g.

Embryos situated near the cloaca were about 2–4 cm larger than those situated near the nidamentary gland. In August and September, but not in April, mean total length per litter increased linearly with total length of the mother (Table 1, Fig. 11). This indicates that embryos grow faster in the larger females.

The weight of 38 large follicles of ovulating females varied from 42 to 56 g. The weight of 59 newly ovulated eggs varied between 40 and 100 g with a mean of 59.4 g, which is the magnitude of the yolk reserve in the egg. From April to September, mean total length and yolkless weight of the embryos increased from 13.3 to 28.0 cm and from 10.0 to 65.0 g, while the weight of the full yolksac decreased from 45 to 17 g. There was no yolksac in a litter of 28 embryos in November. These embryos averaged 30.3 cm TL and 92.9 g total weight. The sex ratio of embryos did not differ significantly from unity: 599 were males and 625 were females.

Cycle of the liver

In sexually immature sharks, the hepatosomatic index (HSI) did not change with body size but varied about the mean of 7.9 throughout the range of total lengths. The HSI of males increased at sexual maturity to a mean of 11.4 (Fig. 12).

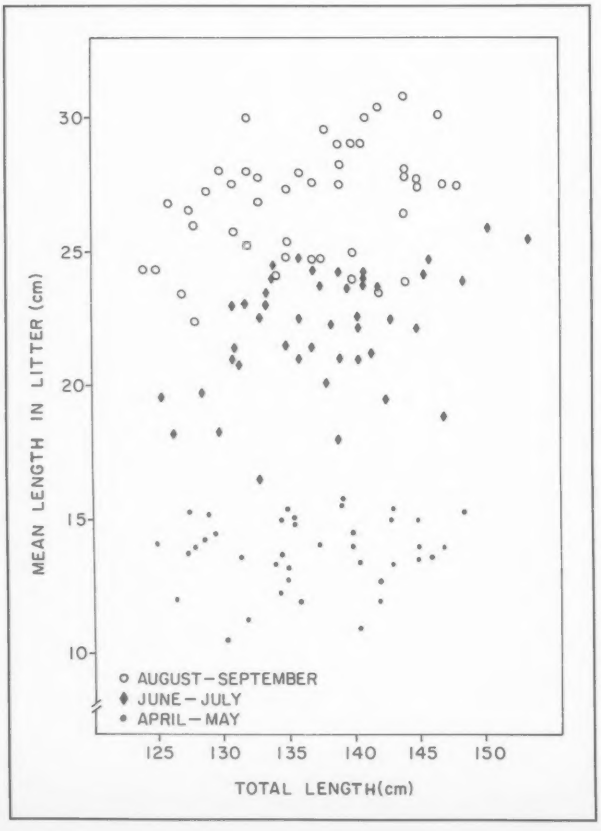


Figure 11
Relationship between total body length of the mother and mean length in litter of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

The HSI of adult females varied during the reproductive cycle; the mean was 7.2 in GR females, 10.8 in NGR-1, and 17.2 in NGR-2 females (Fig. 13). In all categories, the mean monthly HSI decreased from a maximum in early winter to a minimum in spring (Fig. 14).

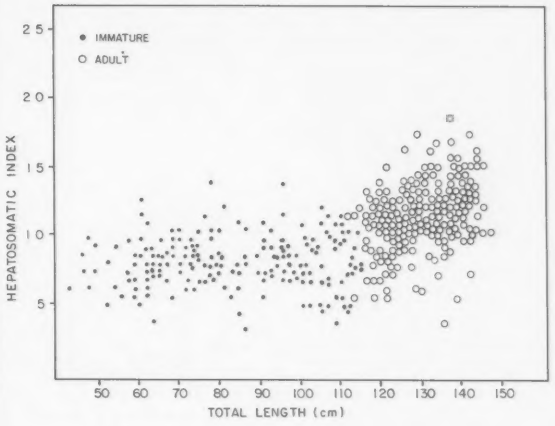


Figure 12
Relationship between total body length and hepatosomatic index of males of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Discussion

Body size at attainment of sexual maturity, as a percent of maximum size, and the slope of the linear regression of fecundity on total length are similar in the western South Atlantic, Australian, and eastern North Pacific populations of the school shark (Table 3, Fig. 15). It is concluded that these parameters of reproduction are characters at the species level.

The dense groups of spermatozoa in the seminal vesicles of adult males of the school shark were designated spermatophores, in analogy with structures described in the basking shark *Cetorhinus maximus* and the blue shark *Prionace glauca* (Matthews 1950, Pratt 1979). During the present study, spermatophores were also found in the seminal vesicle of the smooth dogfish *Mustelus canis* and the sand shark *Eugomphodus taurus*. It seems that the grouping of spermatozoa in dense agglomerations is a commom feature in elasmobranchs.

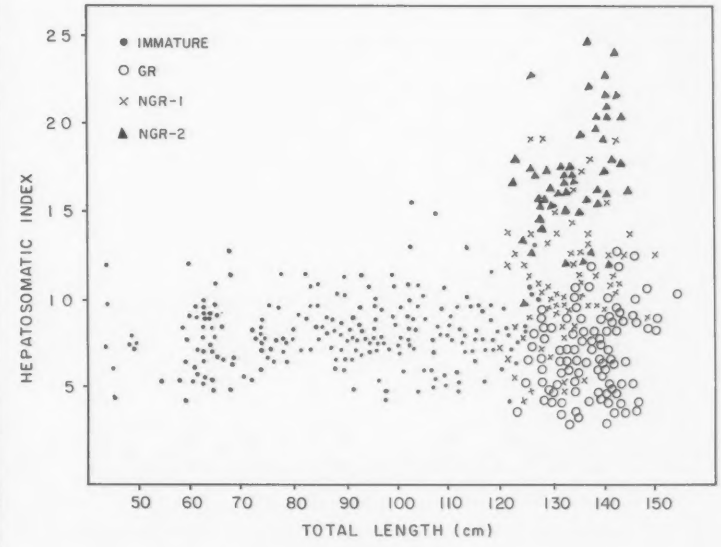


Figure 13
Relationship between total body length and hepatosomatic index of females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil, in different stages of the reproductive cycle. GR, gravid; NGR-1, 1st year nongravid; NGR-2, 2d year nongravid.

There is no discontinuity in the gonadosomatic index of school shark adult males, such as would indicate the simultaneous existence of different reproductive stages, as was observed in females. All smears of the seminal vesicle of adult males in July contained spermatophores. It is concluded that all adult males present in the area during winter are in the mating stage.

In the western South Atlantic population, copulation occurs up to at least 5 months before ovulation. Gestation is highly synchronized, with all phases from ovulation to birth being timed at the population level. This requires that at a particular period each year, all NGR-2 females will have mated and will be ready to ovulate. The extended mating period ensures this. The same is observed in the blue shark, where the female mates up to 12 months before ovulation (Pratt 1979).

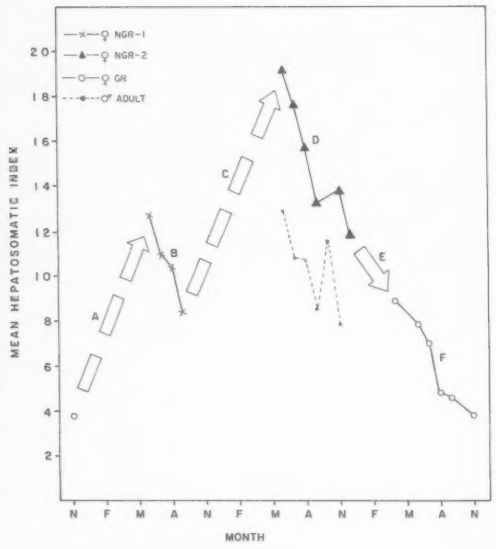


Figure 14

Mean monthly hepasomatic index of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil, in different reproductive stages. GR, gravid; NGR-1, 1st year nongravid; NGR-2, 2d year nongravid.

Table 3

Total length (TL, in cm) and age (years) at stages of sexual development in geographical populations of *Galeorhinus galeus*. Data on the Australian population after Olsen (1984) and on the eastern North Pacific population after Ripley (1946). Age in the western South Atlantic population after growth curve by Ferreira and Vooren (1991). Length ratio expresses TL at first maturity, as a percent of observed maximum values.

	SW Atlantic	Australia	NE Pacific
Male			
TL 1st maturity	107.0	120	135
Age 1st maturity	10.5	8	–
TL 50% maturity	111.0	–	142
Age 50% maturity	11.4	–	–
TL full maturity	117.0	132	175
Age full maturity	13.2	10	–
TL maximum	148.0	155	185
Age maximum	36.1	41	–
Length ratio	72.3	77.4	73.0
Female			
TL 1st maturity	118.0	135	150
Age 1st maturity	14.1	12	–
TL 50% maturity	123.0	–	158
Age 50% maturity	15.7	–	–
TL full maturity	128.0	–	180
Age full maturity	17.5	–	–
TL maximum	154.5	174	195
Age maximum	36.2	53	–
Length ratio	76.1	77.6	76.9

Ripley (1946) concluded that in eastern North Pacific animals, gestation lasts 12 months during which there is no vitellogenesis and that parturition occurs in summer. Data on the female cycle in this population were obtained from a single sampling area where, in a sample of 3747 females, 88% were gravid, 11% had large ovarian follicles, and 1% were resting. The percentages reflect the situation at a certain point of the migration route of the gravid females, but the data indicate the simultaneous presence of three categories of adult females. In winter, Olsen (1954) observed two types of nongravid Australian females: one with the largest ovarian follicles ranging from 4.0 to 5.0 cm in diameter, and the other with maximum follicle diameters of 1.0–2.0 cm. These two categories occurred simultaneously and in similar numbers. Parturition took place in November–December, and size at birth was about 31 cm TL. Olsen (1954) assumed that gestation starts immediately after mating in winter and lasts 6 months. The presence of the two nongravid categories was explained by a period of 18 months for the production of the mature follicle, giving a cycle of 2 years. However, in view of the data on gestation in western South Atlantic and eastern North Pacific animals, it is unlikely that this phase lasts only 6 months in Australian animals. Therefore, we conclude that the duration and timing of the reproductive cycle are similar in these three populations of school shark.

The observed increase in body size of embryos from the anterior to the posterior end of the uterus has also been noted in eastern North Pacific and Australian animals. This may partly reflect duration of the ovulation process, during which eggs enter the oviducts in pairs at intervals of 24–48 hours in the smooth dogfish, in the skates, *Raja brachyura* and *Raja erinacea*, and in the sand shark (TeWinkel 1950, Holden 1974, Gilmore et al. 1983). Assuming an interval of 36 hours in the school shark, the duration of ovulation for all eggs would range between 10 and 40 days, depending on fecundity. The size difference between the first and the last embryo in the uterus would then reflect the growth of the first embryo during the ovulation period, although the possibility of a corresponding difference in yolk reserve remains to be investigated.

In spring, liver weight as a proportion of total body weight (HSI) of the eastern North Pacific adult female NGR-2 was 14%, and about 4% in GR females. In the

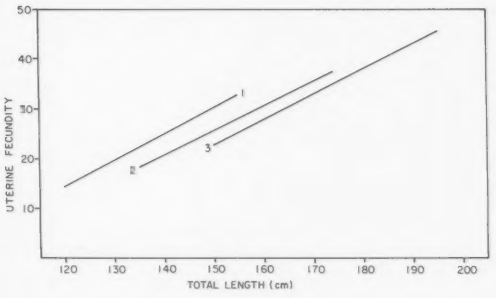


Figure 15

Relationship between total body length and uterine fecundity of the school shark *Galeorhinus galeus*, of (1) southern Brazil; (2) southern Australia, according to Olsen (1984); and (3) California, according to Ripley (1946).

Australian animals, the HSI ranged from 6.0 to 11.0 in GR females, and from 15.0 to 24.0 in NGR-2 females (Olsen 1954). Since these values are similar to those of comparable eastern South Atlantic females, it is concluded that the liver cycle of adult females observed in the present study is characteristic of the species.

When estrogen was administered to the female of the spotted catfish *Scyliorhinus canicula*, the liver increased in size and produced vitellogenin and released it into the blood (Craik 1978). Estrogen is produced by the granulosa of the maturing ovarian follicle of the spiny dogfish *Squalus acanthias*, and by the mature testis of *Torpedo marmorata*, *Scyliorhinus canicula*, *Squalus acanthias*, and *Raja clavata* (Lance and Callard 1969, Craik 1978, Dodd 1983). This explains why in the western South Atlantic school shark the HSI increases in both sexes after sexual maturation and varies with the cycle of the adult ovary, reaching a maximum during the NGR-2 stage. Ripley and Bolomey (1946) show that in spring the proportion of oil in the liver of the eastern North Pacific adult is about 60% in males and NGR-1 females, 40% in GR and postpartum females, and 70% in NGR-2 females and those with uterine eggs. Thus, the changes in HSI of the adult female reflect a major variation in the quantity of lipids in the liver during the reproductive cycle.

The submerged weight (SW_i) in seawater of an object i can be determined by the model

$$SW_i = m_i (1 - d_s / d_i),$$

where m_i is the mass of the object in g, and d_s and d_i are the specific densities of seawater and of the object, respectively, in g/cm^3. A negative submerged weight indicates buoyancy. Using this model, submerged weight for the eviscerated body and the oil reserve in the liver was calculated for males and females of 130 cm TL in all three reproductive stages. For submerged weight of the body, m_i was calculated from the regressions in Table 1, and d_i was estimated at 1.065 g/cm^3, which is the mean of the liver-free body density of 13 species of sharks (Baldridge 1970). For submerged weight of the oil reserve, the liver mass calculated from the HSI in the present study was multiplied by the percentage of oil in the liver in the eastern North Pacific school shark. For the specific density of the liver oil in the different reproductive stages, values from Bone and Marshal (1982) were used: GR females, non-metabolizable lipids, 0.860 g/cm^3; NGR-2 females, metabolizable lipids, 0.930 g/cm^3; NGR-1 and males, the median of these values, 0.895 g/cm^3. To calculate the submerged weights of the mature ovaries of NGR-2 females 130 cm TL, the regression of ovarian fecundity on total length was combined with data on mass and volume of 14 follicles (4.0 cm in diameter).This resulted in an ovary mass of 665.00 g and a specific density of 1.108 g/cm^3. The specific density of seawater was taken as 1.024 g/cm^3, according to Baldridge (1970).

The results are summarized in Table 4. In males and NGR-1 females, the buoyancy of the liver is about one-fourth the submerged weight of the eviscerated body. In NGR-2 females, the increased liver buoyancy compensates for 60% of the submerged weight of the yolk mass in the ovary. Through the production of estrogen, the maturing ovary also controls, simultaneously, the vitellogenic and hydrostatic functions of the liver. Besides providing buoyancy when this is most needed, the metabolic reserve of the NGR-2 female guarantees resources for vitellogenesis and maturation of the follicle, thus ensuring the timing of reproduction.

The specific density of embryos, for example, 1.035 g/cm^3 in the sandbar shark *Carcharinus milberti* (Baldridge 1970), is much less than that of yolk. During gestation of aplacentary sharks, some organic matter in the yolk reserve is lost but water is absorbed, and the full-term embryo weighs twice as much as the yolk (Ranzi 1932). The specific density of the uterus decreases during gestation because of the increase of intrauterine liquid and embryos and the decrease of egg yolk. This enables the gestating female to metabolize her lipid reserves without loss of buoyancy, and explains the low liver buoyancy in this stage. The reduction in liver volume also provides space for the gravid uteri. Such a trade-off between lipids and water without change in overall buoyancy also occurs during the winter fasting of *Clupea harengus* (Iles 1984).

Table 4
Submerged weight of parts of the body in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. NGR-1, 1st year nongravid; NGR-2, 2d year nongravid; GR, gravid.

Item	Submerged weight (g)
Adult male, liver oil	−73.9
NGR-1 female, liver oil	−71.9
NGR-2 female, liver oil	−100.4
GR female, liver oil	−42.3
Adult male, eviscerated body	+288.7
Adult female, eviscerated body	+296.4
NGR-2 female, mature ovary	+50.4

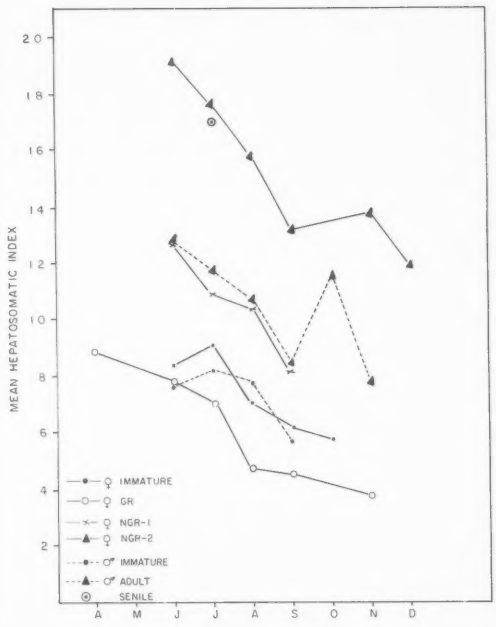


Figure 16
Mean monthly hepatosomatic index during the reproductive cycle of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. NGR-1, 1st year nongravid; NGR-2, 2d year nongravid; GR, gravid. Arrows indicate the hypothetical pattern during periods when the population occurs outside the study area.

The gradual decrease of the HSI in both sexes during winter suggests that at that time, the population invests little effort in feeding and lives mostly off its lipid reserves. From interpolation in the observed HSI pattern, it is concluded that during the first two summers after parturition, the female accumulates lipids. During the third year of the cycle, HSI decreases constantly from ovulation to parturition (Fig. 16). In coastal waters of Uruguay, the species is caught by bottom gillnets during winter and by bottom longlines during summer (De Buen 1952). This is consistent with the hypothesis of the endogenous periodicity of feeding under hormonal control, as in *Clupea harengus* (Iles 1984). It is suggested that in the school shark, feeding during winter is reduced to the intake of proteins necessary for the continuous production of urea. In the liver of the female, a seasonal and a three-year cycle are timed to store and metabolize lipid reserves, to synthesize and transfer vitellogenin, and to control buoyancy, in a sequence which corresponds with the varying physiological needs during the reproductive cycle.

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Differential Selection of Crab *Chionoecetes opilio* and *Hyas* spp. as Prey by Sympatric Cod *Gadus morhua* and thorny skate *Raja radiata*

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Abstract. – During 1981 and 1982, 933 Atlantic cod *Gadus morhua* and 119 thorny skate *Raja radiata* were collected off the northwestern coast of Cape Breton Island, Nova Scotia. Danish seines, jigs, gillnets, and trawls were used for sampling. Stomach contents were analyzed to investigate predator-prey relationships between cod and snow crab *Chionoecetes opilio*, two commercially important species. For comparison, skate and two toad crab species, *Hyas araneus* and *H. coarctatus*, were also considered.

During spring (April, May), cod fed mostly (by weight) on large soft-shelled male snow crab [77–110 mm carapace width (CW)]. In summer (July) and fall (September), cod predation was directed more towards prey species such as fish, although the mean number of snow crab per cod stomach also increased. The average number of snow crab in cod stomach contents was higher (0.59 crab/stomach) on sand and mud bottoms than on rocky and gravel bottoms (0.05 crab/stomach). In contrast, higher numbers of toad crab (1.35 crabs/stomach) were found in stomachs from cod on rocky and gravel bottom than on mud and sand bottom (0.50 crab/stomach).

There were approximately five times more snow crab (by number) in the stomachs of skate than in cod. The frequency of toad crab present in the stomach contents of both predators was similar. On average, individual skate consumed up to five times more snow crab (by number) than toad crab, while cod consumed approximately equal numbers of toad and snow crab. Estimates of crab abundance provide evidence that cod feed more on toad crab than snow crab, whereas skate seem more opportunistic.

Problems associated with using stomach content analysis to assess the potential impact of cod predation on snow crab recruitment are discussed.

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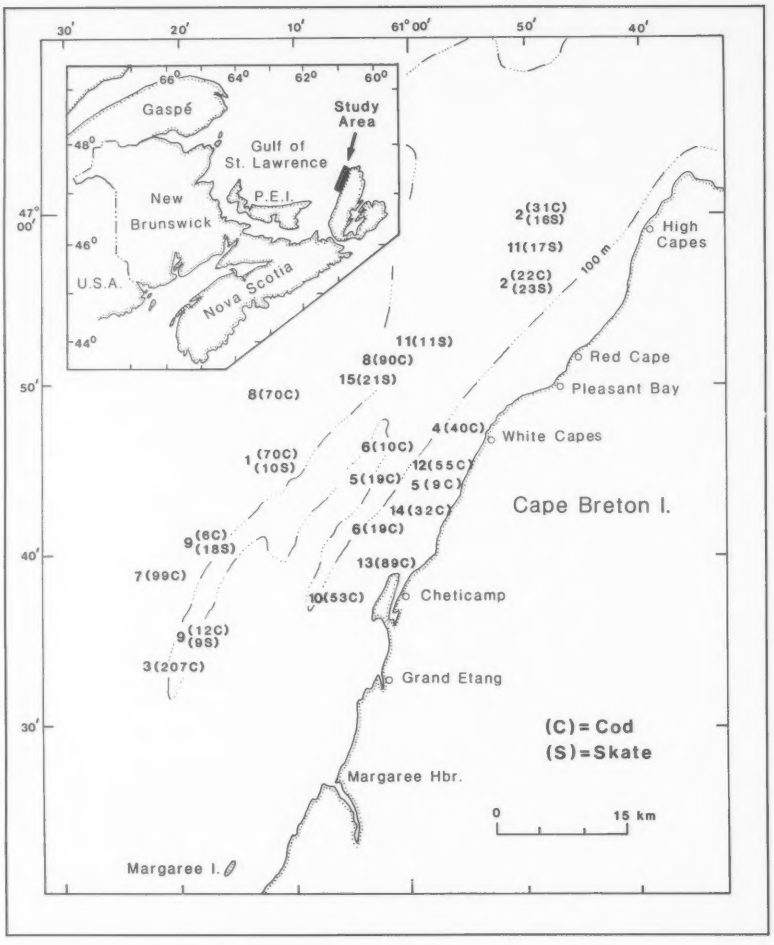
Cod *Gadus morhua* and snow crab *Chionoecetes opilio* which in 1983 supported fisheries valued at $17.4 and $29.1 million, respectively, form two of the most important fisheries in the Gulf of St. Lawrence (Anon. 1982; Elner and Bailey 1986). The snow crab resource is heavily exploited, and the fishery has become almost entirely dependent on the recruitment of crab reaching commercial size each year (Bailey and Elner 1989). Little is known about the factors affecting snow crab recruitment. Past studies on the east coast of Canada have established a predator:prey linkage between cod and snow crab (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982, Lilly and Rice 1983, Lilly 1984, Lilly and Botta 1984, Waiwood and Majkowski 1984). Bailey (1982) suggested that cod predation could be a major factor controlling the number of snow crab entering the fishery each year. However, Waiwood and Elner (1982) suggested that cod do not control recruitment of crab into the fishery, but simply react to the availability of crabs as compared with other prey species.

Although cod has been identified as an important predator of snow crab, the ecological mechanisms involved in the interaction are not well understood. By analyzing cod stomach contents, this work provides fresh insights into cod predation on crab in nature. We also discuss the problems associated with using stomach contents analysis as a means of assessing the impact of cod predation on snow crab recruitment, and evaluate the use of stomach contents as a biological tool for sampling snow crab. For comparative purposes, skate *Raja radiata*, a known predator on crab (Templeman 1982), and two additional crab prey species commonly recognized as toad crab (*Hyas araneus* and *H. coarctatus*) were considered in the study.

Materials and methods

Over the period 21 April 1981 to 29 September 1982, 933 cod and 119

Figure 1
Location of study area and sampling sites during 1981–82. Numbers in parentheses indicate the number of fish sampled, and numbers outside parentheses are sample identification numbers. Data from sites with the same sample number were combined for the analysis.



skate stomachs were collected off the northwestern coast of Cape Breton I. (Fig. 1). Sampling was conducted on an opportunistic basis from various fishing vessels and during research cruises; consequently, different gear types were used (Danish seines, jigs, gillnets, trawls) (Robichaud 1985). Data from samples collected at adjacent sites, on similar bottom, during the same week period and using the same sampling gear were combined and assigned the same sample number (Fig. 1).

Fork length of cod and total length of skate were measured at sea. However, in samples 3 and 8 where large numbers of cod were caught (207 and 160 cod, respectively), all stomachs were removed but, due to limited time, only a random subsample of cod was measured. Possible differences in mean sizes of cod and skate between samples were tested by a "one-way" analysis of variance combined with a Duncan test (Duncan 1955) after transforming the data with Log(x).

Stomach removal was performed by (1) tying off the anterior part of the stomach with plastic "spaghetti" tubing identified by a specimen number, and (2) separating the esophagus in front of the tubing and cutting the posterior part of the pylorus in order to prevent the loss of stomach contents. Stomachs were then preserved in 4% formaldehyde and seawater and transported to the laboratory for analysis. For each cod and skate, data on capture location, depth, bottom type, and gear type were recorded.

In the laboratory, stomach contents were examined and prey remains identified to the lowest taxonomic level that the state of digestion permitted. Food in each taxon was weighed and its contribution, in terms of percent by weight of the stomach contents, was deter-

mined. All unidentified portions and material such as vegetable matter, stones, and mucous were categorized as "others". Empty stomachs, which accounted for less than 9% of the total stomachs sampled, were not used in the analysis. Crab prey were individually identified to species, weighed, measured [carapace width (CW)] and sexed. For each sample, total number of individuals for each crab species, total weight of individuals, frequency of occurrence, and mean number of crabs per stomach were determined. Size-frequency distributions were constructed for each crab species. Relationship between the carapace width of crab and body length of cod or skate predator was also assessed using scattergram plots.

The bottom substrate was sampled using a Van Veen grab. Substrate characteristics were also based on sediment information, collected also with a Van Veen grab, during a juvenile snow crab survey done concurrently with this study (Robichaud 1985, Robichaud et al. 1989).

Results

The average number of *H. araneus* and *H. coarctatus* per cod stomach was 0.37 [variance (S) 1.04] and 0.42 (S 1.82), respectively. Predation by cod on the two toad crab species followed similar patterns. The average number of both toad crab species per cod stomach was higher on gravel bottom [0.59 (S 1.54) and 0.53 (S 1.69) for *H. araneus* and *H. coarctatus*, respectively] and lower on sand and mud bottom [0.19 (S 0.56) and 0.33 (S 1.93) for *H. araneus* and *H. coarctatus*, respectively]. In addition, the number of both toad crab species per skate stomach was low [0.02 (S 0.02) and 0.06 (S 0.16) for *H. araneus* and *H. coarctatus*, respectively]. Because there was no significant differences ($P>0.05$, using t-test) in number per stomach between the two toad crab species, and because of the large proportion (23%) of toad crabs that was unidentifiable and categorized as *Hyas* species, all toad crabs were combined for the stomach analysis.

There were significant differences ($P<0.05$) in the average size of cod between samples (Fig. 2). There were no significant differences ($P>0.05$) in the mean size of skate between samples (Fig. 2).

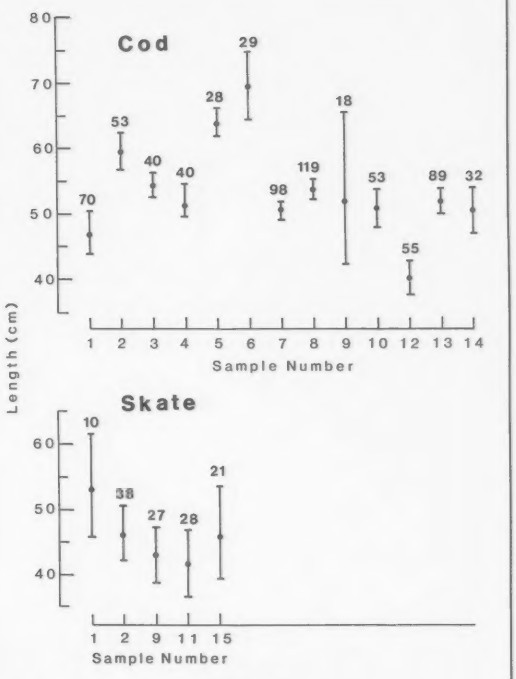


Figure 2

Geometrical mean size of cod and skate for each sample collected during 1981–82. Dots are means; vertical lines are ±95% confidence limits; numbers above dots are the number of fish in each sample.

Cod stomach analyses

The stomach contents of cod caught by Danish seiners or by trawls over deep (100–141 m) muddy or sandy bottoms during the spring of 1981 and 1982 comprised a large percentage by weight of snow crab (Fig. 3; Table 1, samples 1–3). The percentage by weight of snow crab found in cod stomachs ranged between 40.4 and 66.2%. The mean number of snow crab per cod stomach ranged between 0.13 and 0.39, respectively (Fig. 3; Table 1). In the same samples, the percentage by weight of toad crab (*Hyas araneus* AND *H. coarctatus*, combined) ranged between 1.8 and 5.2%, and the mean number of toad crab per cod stomach ranged between 0.10 and 0.53 (Fig. 3; Table 1). The high percentage of the total weight of snow crab in cod stomachs during spring was mainly made up of large soft-shelled males. Whole soft-shelled crabs were usually found compacted into a single pliable ball in cod and skate stomachs. On removal from the stomachs, they could be unfolded and measured. Other prey taxa identified were invertebrates, such as amphipods, euphausiids, and molluscs, and minor quantities of fish (Fig. 3, samples 1–3).

In May 1982, cod taken by jigging over gravel bottom at shallow depth (55 m) contained a negligible amount of snow crab (0.4% of overall weight) (Fig. 3, sample 4). In the same sample, the percentage by weight of toad crab was higher (27.8%) and the mean

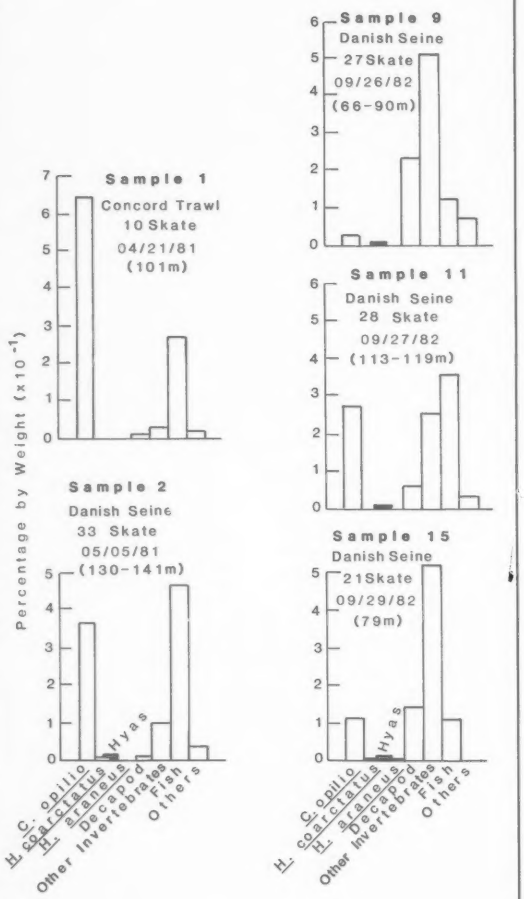


Figure 3

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in April/May 1981 and May 1982. Dark bar represents the percentage by weight of toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*); depth range given in meters.

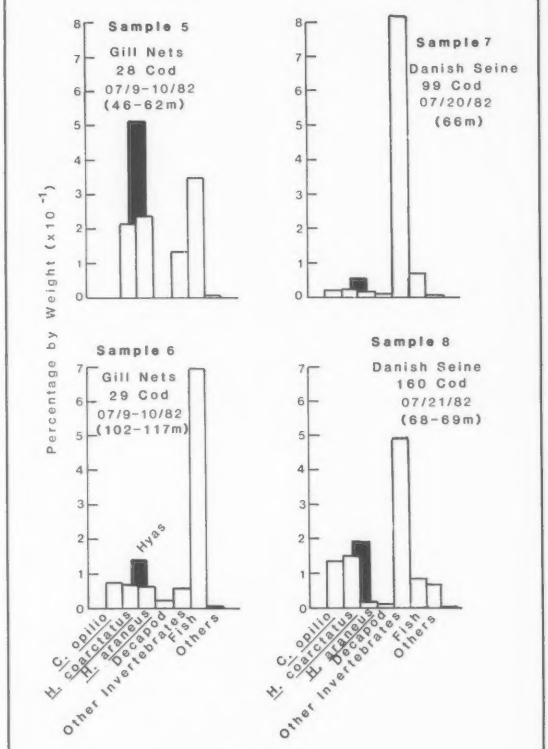


Figure 4

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in July 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

number of toad crab per stomach was 1.63, compared with 0.05 for snow crab (Fig. 3; Table 1). In this sample, there was also a large proportion (39.9%) of other invertebrates consumed.

During July 1982, in cod sample 5, taken with gillnets set on gravel bottom in shallow water (46–62 m), there were no snow crab (Fig. 4). However, the percentage by weight of toad crab was 51.2%, and the average number of toad crab per cod stomach was 2.0. For sample 6, from the stomach contents of cod also captured by gillnets, but in deeper water (102–117 m) on mud bottom mixed with boulders, the percentage by weight of snow crab was 7.4% and the mean number of snow crab per cod stomach was 0.17 (Fig. 4; Table 1). In comparison with sample 5, the percentage by weight of toad crab in sample 6 decreased to 14.7% and the mean number of toad crab per cod stomach was 1.65 (Fig. 4; Table 1). In cod samples 5 and 6, the major diet percentages of total weight were fish (34.7 and 69.6%, respectively) such as pleuronectids and gadids (Fig. 4).

In July 1982, for stomachs of cod taken by Danish seiners over shallow (66–69 m) sandy and muddy bottoms (Fig. 4, samples 7 and 8), the percentage by weight of snow crab was 2.2 and 13.8%, respectively. This percentage of total weight was lower than that found in cod stomachs taken on similar but deeper (101–141 m) bottoms during spring 1981 and 1982 (Fig. 3, samples 1–3). However, the mean number of snow

Table 1

Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in cod stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight		Frequency of occurrence		Mean number per stomach	
				Snow crab	Toad crab	Snow crab	Toad crab	Snow crab	Toad crab
1	101	04-21-81	70	40.4	5.2	8.6	4.3	0.13	0.10
2	130–141	05-05-81	53	59.2	4.5	26.4	13.2	0.38	0.53
3	101	05-10-82	207	66.2	1.8	33.3	8.7	0.39	0.19
4	55	05-28-82	40	0.4	29.8	2.5	36.9	0.05	1.63
5	46-62	07-9/10-82	28	—	51.2	—	53.6	—	2.00
6	102–117	07-9/10-82	29	7.4	14.7	10.3	48.3	0.17	1.65
7	66	07-20-82	99	2.2	5.7	30.3	18.2	0.47	0.37
8	69	07-21-82	160	13.8	18.1	52.5	42.5	1.16	1.16
9	66–90	09-26-82	18	24.5	16.1	27.8	16.7	0.78	0.22
10	51	09-26-82	53	0.1	40.8	7.5	52.8	0.08	1.57
12	46	09-27-82	55	—	48.8	—	49.1	—	1.96
13	46	09-28-82	89	0.1	5.5	1.1	27.8	0.01	0.49
14	33	09-28-82	32	—	9.7	—	25.0	—	0.78

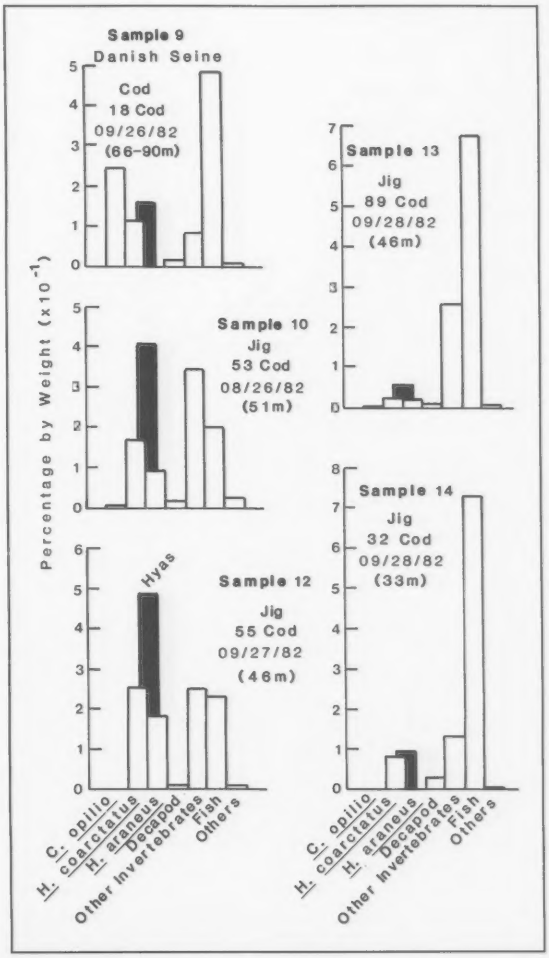


Figure 5

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

crab per cod stomach for samples 7 and 8 had increased to 0.47 and 1.16, respectively (Table 1). The percentage by weight of toad crab in cod samples 7 and 8 was 5.7 and 18.1%, respectively. The mean number of toad crab per cod stomach (0.37 and 1.16 crab/stomach, respectively) was similar to the mean number of snow crab found in the same cod stomach samples (0.47 and 1.16 crab/stomach, respectively) (Fig. 4; Table 1). In samples 7 and 8, cod had concentrated their feeding on other invertebrates (49.7 and 82%, respectively) such as euphausiids, gastropods and polychaetes.

During September 1982, in cod sample 9, taken by Danish seiners on muddy or sandy bottom at intermediate depths (66–90 m), the percentage by weight of snow crab was 24.5%, and the mean number of snow crab per stomach was 0.78 (Fig. 5; Table 1). The increase in the percentage by weight of snow crab in September is a consequence of a size increase of juvenile crab ingested in September (13.2 g/crab) compared with July (3.7 g/crab). The percentage by weight of toad crab in sample 9 was 16.1%, and the average number of toad crab per cod stomach was 0.22 (Fig. 5; Table 1). The largest percentage of total weight in sample 9 was composed of fish (48.6%) such as mackerel *Scomber scombrus*, pleuronectids, and smaller gadids.

Cod captured with jigs at sites a few kilometers from shore on shallow (46–51 m) gravel bottom (samples 10 and 12) consumed negligible amounts of snow crab (Fig. 5; Table 1). In contrast, the percentage by weight of toad crab in samples 10 and 12 was 40.8 and 48.8%, respectively, and the mean number of toad crab per cod stomach was 1.57 and 1.96, respectively (Fig. 5; Table 1). Other important prey in the diet of these cod were invertebrates (25.4 and 34.7%) (amphipods, euphausiids, and molluscs) and fish (20.2 and 23.3%) [pleuronectids, mackerel *Scomber scombrus*, and small gadids].

Cod captured with jigs at sites closer to shore on shallower (33–46 m) gravel bottom (samples 13 and 14) also consumed negligible amounts of snow crab (Fig. 5; Table 1). However, the percentage by weight of toad crab was lower, 5.5 and 9.7%, as was the mean number per stomach, 0.49 and 0.78 (Fig. 5; Table 1). In addition, stomachs contained *Cancer* crab and a lobster *Homarus americanus*, but the main prey once again was fish (67.7 and 73.2%) (Fig. 5).

Skate stomach analyses

All skate were collected during spring 1981 and fall 1982 by Danish seines or concord trawls over sandy and muddy bottoms (Fig. 1) (samples 1, 2, 9, 11, and 15). During spring 1981 (samples 1 and 2), the percentage by weight of snow crab found in skate stomachs was 37.7 and 64.3%, and the mean number of snow crab per stomach was 0.30 and 2.26 (Fig. 6; Table 2). The large percentage by weight of snow crab present was large soft-shelled males. Besides crab, skate fed on fish (27.4 and 46.9%) such as cod, hake *Urophysis tenuis*, herring *Clupea harengus*, and sand lance *Ammodytes americanus*.

During September 1982 (samples 9, 11, and 15), the percentage by weight of snow crab had decreased to between 3.5 and 27.6%, but the mean number of snow crab per skate stomach had increased to between 1.44 and 4.81 (Fig. 6; Table 2). The overall average number of crab per stomach was twice as high during the fall as in spring. During fall 1982, skate diet also included large quantities of other invertebrates (up to 52%) (polychaetes, amphipods, euphausiids, gastropods, cephalopods, hermit crab *Pagurus longicarpus*, and brittle stars *Ophiopholis aculeata*) and fish (up to 35%) (Fig. 6) such as mackerel *Scomber scombrus* and pleuronectids.

Comparisons between cod and skate as crab predators

The percentage by weight of toad crab in the diet of skate was small (0–1.3%) (Fig. 6; Table 2). However,

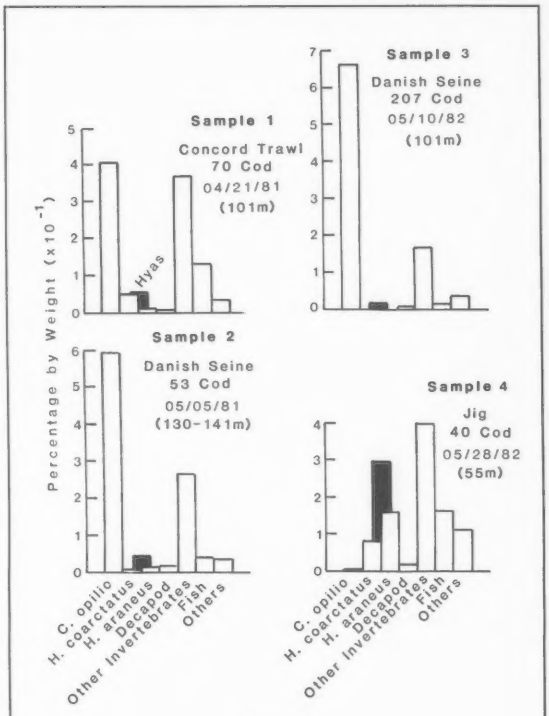


Figure 6

Percentage by weight of prey categories against total weight of stomach contents from skate sampled in April/May 1981 and September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

the mean numbers of toad crab per stomach for cod and skate captured at the same sampling sites in the same tows were similar (0.28 and 0.30 for cod and skate, respectively) (Table 3, samples 1, 2, and 9). In these same samples, the mean number of snow crab found in skate stomachs was on average 4.9 times higher than the mean number of toad crab (Table 3), whereas the mean numbers of snow crab and toad crab found in cod stomachs were similar (0.30 and 0.28, respectively). Skate also appeared to consume up to five times more snow crab than cod (1.60 and 0.30 per skate and cod, respectively) (Table 3).

Influence of season and substratum type

The quantity of crab consumed by cod varied between bottom types. In the stomachs of cod captured on sand and mud bottoms, the overall mean numbers of snow crab and toad crab per stomach were generally similar

Table 2

Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in skate stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight		Frequency of occurrence		Mean number per stomach	
				Snow crab	Toad crab	Snow crab	Toad crab	Snow crab	Toad crab
1	101	04-21-81	10	64.3	—	40.0	—	0.30	—
2	130–141	05-05-81	33	37.7	0.7	75.8	30.3	2.12	0.58
9	66–90	09-26-82	27	3.5	0.2	51.9	14.8	1.44	0.15
11	113–119	09-27-82	28	27.6	0.05	85.7	3.6	4.64	0.04
15	79	09-29-82	21	11.8	0.01	100.0	4.8	4.81	0.05

Table 3

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod and skate stomach for fish captured in the same tows.

Sample no.	Cod			Skate		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
1	70	0.13 (0.26)	0.10 (0.29)	10	0.30 (0.45)	—
2	53	0.38 (0.90)	0.53 (3.65)	33	2.12 (5.81)	0.58 (1.12)
9	18	0.78 (3.13)	0.22 (0.30)	27	1.44 (4.04)	0.15 (0.13)
Total	141	0.30 (0.88)	0.28 (1.56)	70	1.60 (4.67)	0.33 (0.62)

Table 4

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod stomach for fish captured by bottom type and seasons.

Season	Sand and mud bottom			Gravel, rocky bottom		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
Spring	330	0.35 (0.52)	0.23 (1.12)	40	0.05 (0.12)	1.63 (6.76)
Summer	259	0.90 (1.82)	0.86 (6.97)	57	0.09 (0.18)	1.82 (7.43)
Fall	18	0.78 (3.13)	0.22 (0.30)	229	0.02 (0.02)	1.14 (5.26)
Total	607	0.59 (1.21)	0.50 (3.69)	326	0.04 (0.06)	1.35 (5.86)

except in the fall. However, the fall sample was small (Table 4). On rocky and gravel bottoms, toad crabs were much more abundant (Table 4). Furthermore, the overall mean numbers of snow crab per stomach from cod captured on mud and sand bottoms were substantially greater than for cod captured on gravel and rocky bottoms. For toad crab, mean numbers per stomach were higher in cod captured on rocky and gravel bottom than from sand and mud bottoms.

Crab:cod size relationship

Three distinct size groups of snow crab were detected (Fig. 7). One group, found only during the spring sampling, was comprised mainly of recently molted males ranging in size between 77 and 107 mm CW (Fig. 7). These soft-shelled crabs were consumed by cod ranging in size between 49 and 66 cm (Fig. 7). The second group of snow crab comprised hard-shelled adult females with eggs. This group of crabs was consumed only by larger cod ranging in size between 67 and 106 cm (Fig. 7). The third and most numerous group of

snow crab found in cod was made up of juveniles (of both sexes) ranging between 6 and 44mm CW. These smaller crabs were found in stomachs of cod ranging between 33 and 82cm. The size range of juvenile crab consumed by cod appeared to broaden with cod size (Fig. 7). However, the pattern seems to reach a plateau for juvenile crab above 44mm CW; larger juveniles were not found even in large cod. Larger crab or alternate prey species were present in the stomach contents of cod above 82cm.

The relationship between the size range of the two *Hyas* species and cod length was similar to the relationship found between snow crab and cod (Fig. 8). The size range of toad crab consumed became broader as cod size increased. However, no toad crab over 46mm CW were found.

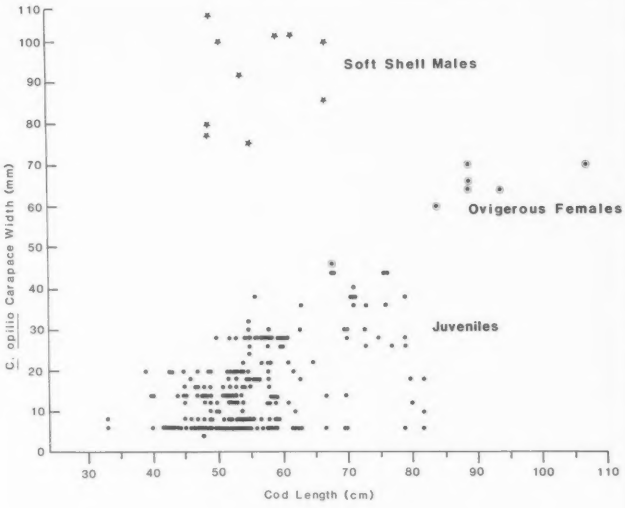


Figure 7
Relationship between carapace width (mm) of *C. opilio* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

Crab:skate size relationships

The relationship between skate length and the size of snow crab consumed appears different from the relationship between snow crab and cod (Fig. 7 and 9). The size range of juvenile snow crab consumed by skate is narrower, with no juveniles larger than 27mm CW present, compared with 44mm CW for juvenile crabs found in cod stomachs. Nevertheless, during the spring of 1981, two large soft-shelled male snow crab were found in skate stomachs, indicating that skate were able to feed on larger snow crab (Fig. 9).

The number of toad crab present in skate stomachs was small (Fig. 9). The size range consumed was narrow (5–21mm CW) and did not change with skate size.

Size-frequency distributions of crab prey

By visual inspection, up to six distinct size-classes, or molt groups, were determined for snow crab found in cod stomachs (Fig. 10). Five of these molt groups could be correlated to molt groups determined by Robichaud et al. (1989) for snow crab caught by beam trawling during the same period in the same area. The corresponding mean sizes for each of the molt groups were 6.8, 13.9, 19.6, 27.1, and 37.3mm CW. Only two corresponding molt groups (6.8 and 13.9mm CW) could

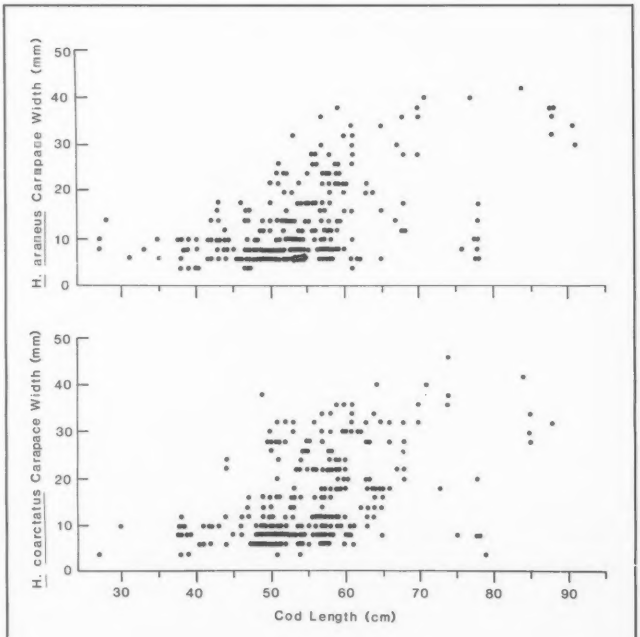


Figure 8
Relationship between the carapace width (mm) of *Hyas araneus* and *H. coarctatus* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

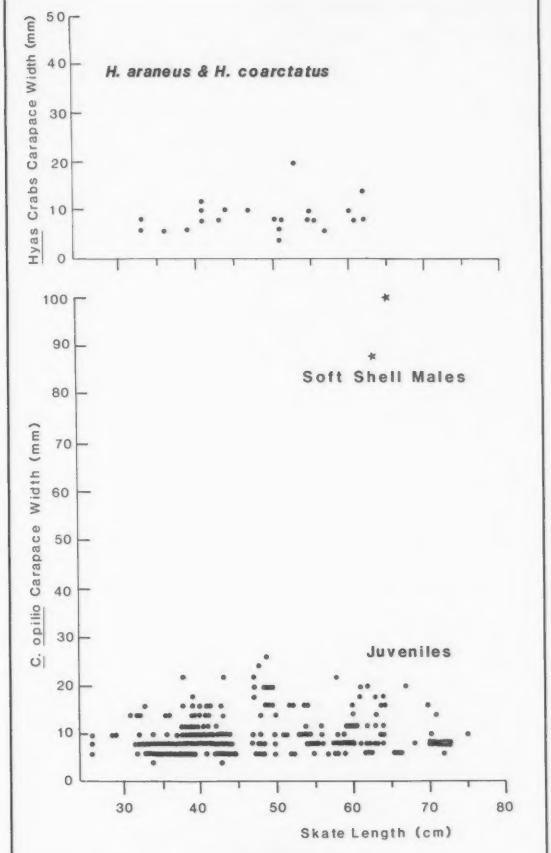


Figure 9

Relationship between the carapace width (mm) of *Hyas araneus*, *H. coarctatus*, and *C. opilio* found in the stomachs of skate sampled in April/May 1981 and September 1982, and the overall length (cm) of the skate.

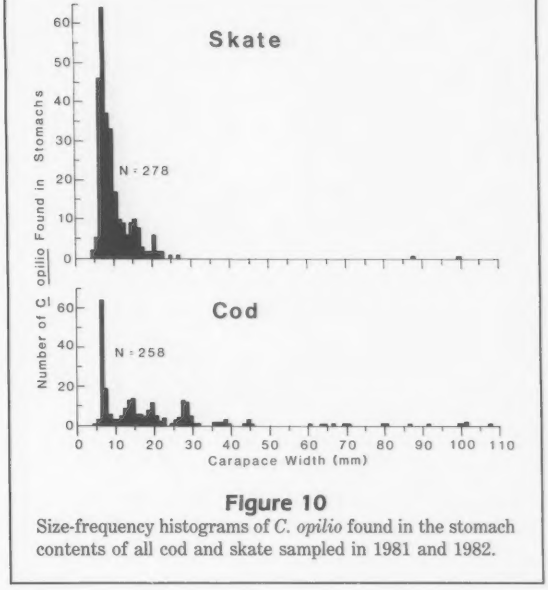


Figure 10

Size-frequency histograms of *C. opilio* found in the stomach contents of all cod and skate sampled in 1981 and 1982.

be identified from snow crab found in skate stomachs (Fig. 10).

The size-frequency distributions of *Hyas araneus* and *H. coarctatus* found in cod stomachs were similar (Fig. 11). However, although molt groups could be determined visually, detailed modal analysis of the distributions was not possible because of the small number of individuals comprising each mode (Macdonald and Pitcher 1979). The maximum size of *Hyas araneus* and *H. coarctatus* found in cod stomachs was 42 and 46 mm CW, respectively.

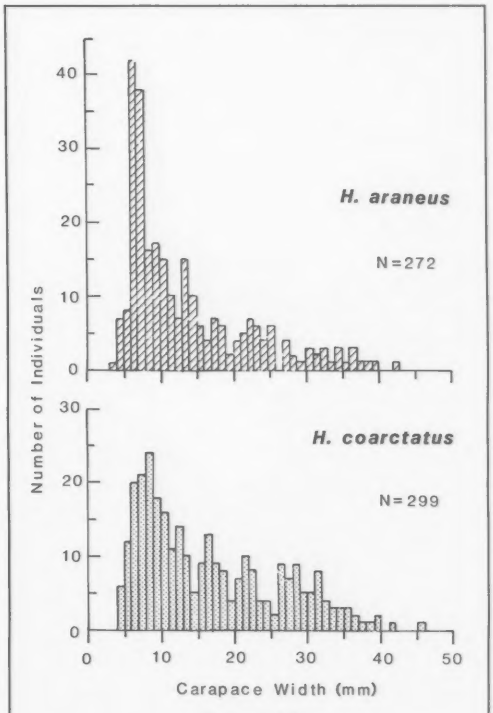


Figure 11

Size-frequency histograms of toad crab found in the stomach contents of all cod sampled in 1981 and 1982.

Discussion

Our study indicates that the diets of cod and skate vary according to season and bottom type. Although there were significant differences ($P<0.05$) in the mean size of cod between some samples which could create some bias in the analyses, the changes in the diet of cod appeared to follow the same general pattern between season and bottom type independent of cod size in each sample (Fig. 2). During spring, cod fed on large soft-shelled male snow crab, while during summer and fall, predation was directed more towards alternate prey species, such as fish and other invertebrates. Seasonal variations in cod diet could reflect the abundance and availability of potential prey species. Such a hypothesis is in accord with Lacroix and Marcotte (1962), Kinnear and Livingstone (1979), Kohler and Fitzgerald (1969), and Corbeil (1954), who argued that seasonal and regional variations in the quantity of prey species eaten by cod are probably due to the distribution of individual prey species, and that prey choice in cod is influenced by prey size, availability, abundance, and ease of capture. Thus, our results may reflect the relative densities and size composition of each crab species present at each sampling site at given times. We found that snow crab were more numerous in cod stomachs from sand and mud bottoms located offshore (0.59 crab/stomach) than on inshore rocky and gravel bottom (0.05 crab/stomach). In contrast, larger numbers of toad crab (1.35 crab/stomach) were found on rocky and gravel bottoms inshore than on mud and sand bottoms offshore (0.50 crab/stomach). We also determined that the two *Hyas* species were present in cod stomachs at similar densities (0.37 *H. araneus* and 0.42 *H. coarctatus*/cod stomach), regardless of bottom type.

Cod and skate appeared to have different feeding patterns for crabs. On average, skate consumed five times more snow crab (1.60 crabs/stomach) than toad crab (0.33 crab/stomach). In contrast, cod captured in the same tows as skate consumed equivalent numbers of snow crab (0.30 crab/stomach) and toad crab (0.28 crab/stomach). Based on a beam trawl survey in the same area during the same periods, Robichaud et al. (1989) determined that snow crab density (11.4 crabs/1000 m^2) was four times higher than the density of toad crabs (2.8 crabs/1000 m^2). If beam trawling is considered to be an unbiased sampling method reflecting the actual densities of both crab species in the area, we can argue that cod feed more on toad crab than snow crab. In contrast, skate would appear to be a more opportunistic predator, feeding on snow crab and toad crab in direct proportion to their actual occurrence.

The stomach contents of cod and skate probably reflect different foraging modes. Cod detect their prey by visual and olfactory cues, but are not capable of detecting buried prey (Brawn 1969). Since snow crab can bury themselves in sediment (Brunel 1960, Miller 1975), cod may experience difficulty in locating them. In comparison, toad crab appear to depend on camouflage rather than burial for protection (D.A. Robichaud, pers. obs.) and are usually found at the sediment surface. As skate prefer foraging in sediment (McEachran et al. 1976), it should be possible for them to detect snow crab buried in mud and sand. In addition, they would also, presumably, be able to locate toad crab on the surface. However, skate may not be as good at catching crabs on the surface.

When attempting to elucidate the impact cod predation could have on snow crab recruitment, many ecological factors need to be considered: distribution patterns of the predator and prey in time and space, size of the predator and prey, availability and vulnerability of the prey, presence of alternative prey species; and behavior of predator and prey. However, one other important non-ecological factor which may influence one's assessment of the relative importance of a prey species in a predator's diet is the method of stomach content analysis employed by the investigator. Different methods of analysis can lead to markedly different conclusions (Hyslop 1980). For example, in this study, if we consider only weight as a measure of the importance of snow crab in cod diet, the greatest quantity of crab present in cod stomachs was during the crab molting period in spring. However, if we consider the actual number of snow crab per stomach or their frequency of occurrence, the number of crab eaten during summer (0.90 crab/stomach) was almost three times higher than spring (0.33 crab/stomach) and the frequency of occurrence was almost twice the spring level (44% vs. 27% in spring). During spring, cod ate fewer but larger soft-shelled male snow crab. During summer and fall, even though the percentage by weight of snow crab was much lower, cod consumed more numerous small juvenile crabs.

Although there are constraints to the present analysis (for example, sampling method, fish size, and the small number of samples), the results provide insight into the predator:prey relationships between fish and crab. However, given the constraints and based on the statistical advice provided, it was decided that any additional effort to statistically isolate the influence of single independent variables such as gear type, season, predator size, depth, or substrate would not only be inappropriate, but liable to create misleading conclusions. For example, studies by Powles (1968), Brêthes et al. (1987), Coulombe et al. (1985), and Robichaud et al. (1989) have shown that substrate is a more important influence than depth on snow crab distribution. We stress that depth, although it may be correlated

strongly with crab density, is secondary to substrate type. Studies by Robichaud (1985) and Robichaud et al. (1989) have shown that snow and toad crab densities were not significantly different over a wide depth range for a given substrate and crab species. A study by Scott (1982) on selection of bottom type by 25 species of groundfish, including cod and skate, concluded, even for species like skate which were not strongly associated to bottom type, that depth was not a specific determinant of distribution.

Previous studies on the impact of cod on snow crab recruitment have not taken into account the behavioral and ecological aspects of the two species (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982). The dynamics of benthos:fish trophic interrelationships are complex, and models based on simple expansion of predator abundance and feeding rate data cannot adequately express the "real world" situation.

Acknowledgments

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Population Structure, Ageing, and Fishing Mortality of the New Zealand Abalone *Haliotis iris*

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Abstract. – Populations of the New Zealand (NZ) black-footed abalone *Haliotis iris* were examined in two important fishing areas. Size-frequencies were compared among three regions around Stewart Island in the extreme south of NZ, three regions of the Marlborough Sounds in the northern part of the South Island, and a site closed to commercial fishing in the North Island. Von Bertalanffy growth parameters were estimated from shell growth rings of subsamples from all regions. Mark-recapture data were available for two regions, and independent estimates of von Bertalanffy parameters were calculated. Total mortality was estimated from catch curves and also from length-frequencies using the method of Fournier and Breen (1983). Yield-per-recruit (YPR) and egg-per-recruit (EPR) were calculated and two reference levels of fishing mortality, $F_{0.1}$ and $F_{25\%}$, were estimated. Analyses showed that, despite previous evidence to the contrary, rings are not laid down annually in the regions we examined. For two fishing regions, the estimated current fishing mortality rates are greater than both $F_{0.1}$ and $F_{25\%}$, suggesting that the current fishery is more intense than can be sustained in the long term. YPR and EPR do not appear to be greatly affected by changing the minimum legal size. By decreasing F to $F_{0.1}$, however, equilibrium egg production would increase from 18% to a more satisfactory level with little change in YPR. We discuss management strategies and argue that it would be prudent to decrease fishing mortality, thereby maintaining higher egg production at little sacrifice of YPR.

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Fishery Bulletin, U.S. 89:681–691 (1991).

The fishery for the abalone *Haliotis iris* (called "paua" in New Zealand) is now one of the largest abalone fisheries in the world, yet the biological basis for its management has only recently been examined in detail. Both the minimum legal size (MLS) for fishing and the permissible catch level were arbitrarily set for historical reasons that did not take into account the best yield and egg production of the fishery. Recent research has aimed at assessing whether the present levels of fishing are sustainable.

Individual Transferable Quotas (ITQs) for paua were implemented in 1986 and a Total Allowable Commercial Catch (TACC) was set in each of seven Quota Management Areas (QMAs), based on the previous catch histories of commercial fishers (Schiel 1991). The total catch of paua for the entire country is currently 1193 tons (whole weight).

Haliotis iris is a shallow-water species, endemic to New Zealand (NZ). It occurs around the entire coastline, but is most abundant in the cooler waters from Cook Strait southwards. It is found predominantly at depths of <5 m (Schiel, unpubl. data). Fishing is restricted to free-diving, and no underwater breathing apparatus is allowed. Paua reach 195 mm (shell length) and the MLS is 125 mm. The commercial value of the fishery has increased dramatically during the last five years (Schiel 1991). There are also a large recreational fishery and a continuing importance of both paua meat and shell to the indigenous Maori people.

The history of abalone fisheries worldwide shows that management is difficult and that populations are often overfished, causing a precipitous drop in commercial landings (Sloan and Breen 1988). The difficulties in management arise from the spatial patchiness and sedentary nature of abalone (Poore 1972b, Shepherd 1986, Sluczanowski 1986), an uncertain relationship between standing stock and recruitment (Prince et al. 1988, Breen 1991), and often a paucity of useful information on growth and mortality (Shepherd and Breen 1991). These uncertainties also apply to the NZ paua fishery, which occurs over most of the coastline including many remote places with rough sea conditions and difficult access.

Although the fishing of paua goes back to pre-colonial times (Best 1929), there is a relatively small history of research on the fishery (Schiel 1991). Growth and mortality rates have been studied for only a few sites in the South I. (Poore 1972a, Sainsbury 1982). Estimates of basic

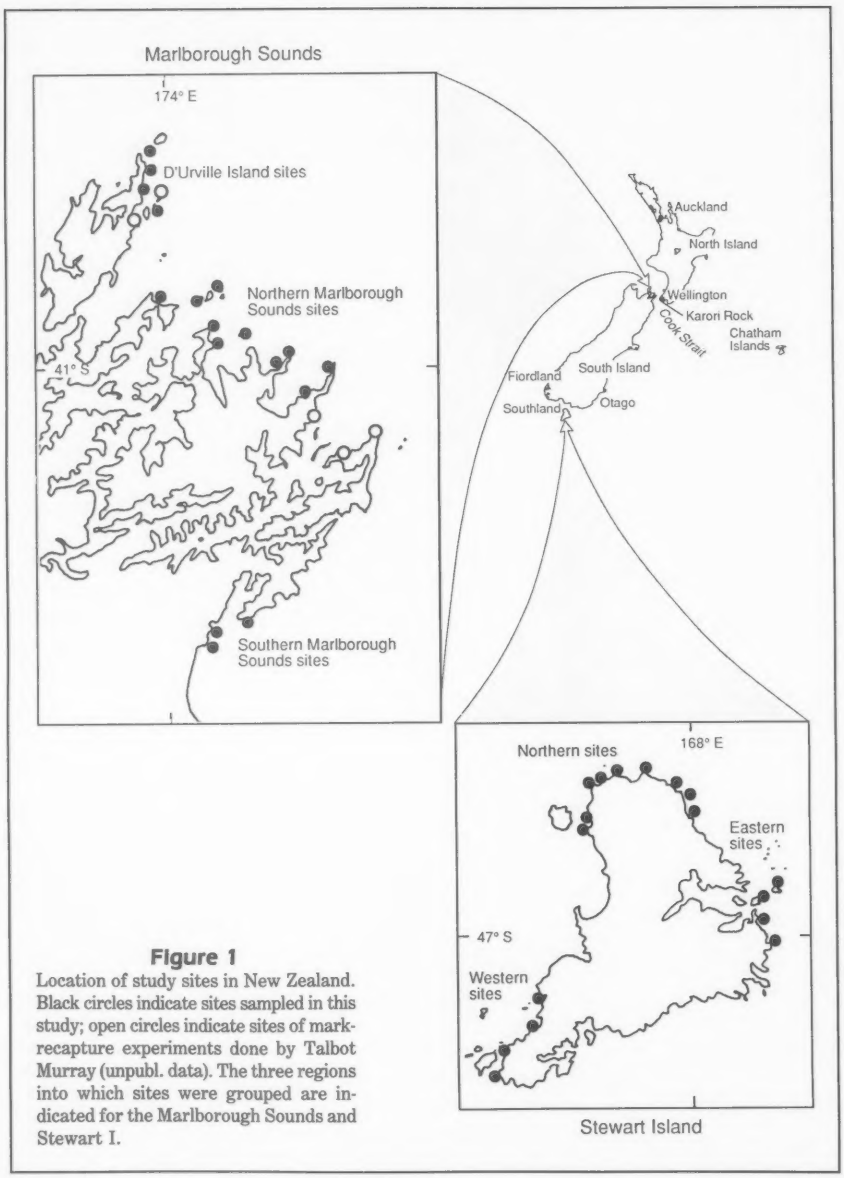

Figure 1
Location of study sites in New Zealand. Black circles indicate sites sampled in this study; open circles indicate sites of mark-recapture experiments done by Talbot Murray (unpubl. data). The three regions into which sites were grouped are indicated for the Marlborough Sounds and Stewart I.

population parameters are required to manage the fishery effectively. In this paper we assess the size structure, age structure, and mortality of paua populations.

We estimate 'age' from growth rings in shells and assess the usefulness of this ageing technique for paua. This is potentially one of the most powerful tools available for estimating growth and mortality rates (Shepherd and Breen 1991). Cross sections of *H. iris* shells have obvious rings. These have previously been used to estimate age and growth (Murray and Akroyd 1984, Murray 1986, Hahn 1989), but no verification has been reported. Similar rings have been used elsewhere to age abalones. For instance, rings in *H. tuberculata* (in the English Channel) have been verified by growth studies (Forster 1967, Hayashi 1980). Verification is also reported in Japanese *H. discus discus* (Kojima et al. 1977) and the Korean *H. diversicolor diversicolor*

and *H. d. aquatilis* (Kim and Cheung 1985). Inoue and Oba (1980) suggest that shell circuli are annual for Japanese *H. gigantea*. Prince et al. (1988) describe a method for ageing Tasmanian *H. rubra*, based on the method of Munoz-Lopez (1976).

In two quota management areas that support substantial landings, we compare estimated levels of fishing mortality with estimates of appropriate levels of fishing mortality obtained from per-recruit modeling. We also compare growth and mortality estimates from shell growth rings with those obtained from other methods. Finally, we explore the consequences of altering the present MLS.

Materials and methods

Field sampling

The size structure of emergent *H. iris* populations was examined around Stewart I., which comprises a major part of the southern fishery, and the Marlborough Sounds, which are a major part of the fishery in the northern part of the South I. (Fig. 1). Stewart I. is exposed to a range of weather conditions. The east coast is in the lee of prevailing westerly winds, but is occasionally subjected to severe easterly storms. The west coast of the island is often inaccessible due to the prevailing winds and a large onshore swell. During the time of our sampling, the swell was reduced to about 1 m. The northern side of the island is protected from the westerly winds but has a refracted westerly swell. Paua occur along the entire coastline of Stewart I.

The Marlborough Sounds are generally less exposed than Stewart I. Paua occur only at the outer margins of the Sounds, as the inner shores are protected and provide generally unsuitable habitat for paua. Northerly winds funnelling through Cook Strait are occasionally severe and can bring exposed conditions to most places where paua are fished. The eastern side of D'Urville I. is protected from westerly winds. Sites in the central portion of the Sounds are generally subjected to similar conditions of exposure to the north, while southeastern sites are protected from the west and north. One other site was used in this study.

Karori Rock is on the south coast of the North I. It is within an area closed to commercial fishing since 1974 after severe depletion of paua populations caused by both commercial and recreational fishing. This site is generally protected from severe swells but occasionally experiences severe northerly and southerly storms in Cook Strait.

Except at Karori Rock, sampling sites were chosen to be representative of commercially harvested sites. This was done in consultation with commercial divers and, at Stewart I., a commercial diver assisted us in the field. During 15–25 September 1989, 17 sites were assessed at Stewart I., and 19 sites during 17–23 October 1989, at the Marlborough Sounds. Karori Rock was sampled on 30 November 1989. Each sampling site was roughly 1 ha in area. Paua were collected, taken to a boat, measured to the nearest mm (shell length), and a subsample from each site was frozen and taken back to Wellington for weighing and ring counting. Remaining paua were returned to their habitat. The numbers collected at each site varied (range 125–548), depending on sea conditions and the abundance of paua. The goal was to collect several hundred paua at each site. To remove paua, we used a blunt trowel of a type commonly used by commercial divers, and took care not to cause damage. Paua less than 70 mm were not representatively sampled because they occupy cryptic inshore habitats and require different sampling techniques. We attempted to sample paua >70 mm representatively by having each diver remove all paua as they were encountered. A total of 5790 (Stewart I.) and 8731 (Marlborough Sounds) paua were measured.

For analyses, we grouped sites by regions of Stewart I. and the Marlborough Sounds (Fig. 1) because we did not wish to assess fine-scale variability in parameters.

Ageing and growth

Shells in the ring-count subsample were measured in length and then sectioned sagittally through the spire with a lapidary saw. Because the rings are obvious (Fig. 2) no further enhancement was necessary. Ring counts for all shells were done by the same experienced technician.

From the ring-count sample data we estimated the von Bertalanffy growth parameters with the non-linear least-squares procedure FISHPARM (Saila et al. 1988). We also estimated growth parameters from mark-recapture data obtained at several sites (Fig. 1) in the northern Marlborough Sounds and around D'Urville I. (Talbot Murray, Min. Agric. Fish., P.O. Box 297, Wellington, pers. commun.). Abalone had been collected, tagged with a numbered plastic disc attached to the shell with epoxy putty, replaced, and recovered later. Most of the times-at-liberty were one year; increments for shorter and longer times (range 92–519 days) were adjusted *pro rata*. We estimated asymptotic length L_∞ and the Brody growth coefficient K from a Ford-Walford regression (Ricker 1975). For comparison with these results, we also calculated growth parameters from age estimates (ring counts) obtained from abalone in the same experiments (Talbot Murray, pers. commun.). The ring counts were done by the same technician, as explained above.

Figure 2
Growth rings in a cross section of a *Haliotis iris* shell.

Mortality estimation

Age-length keys (Ricker 1975) were constructed from the ring-count data. The keys were used to estimate the catch curve from the length-frequency sample for each region; total mortality rate was then estimated from the regression of the natural log of estimated number-at-age on 'age' (Robson and Chapman 1961). The first 'age' included in the procedure was chosen to represent the first 'age' class with a mean length greater than minimum legal size.

Total mortality rates were also estimated from the length-frequency samples using the method of Fournier and Breen (1983), using a strategy similar to that of Tegner et al. (1989). To obtain the fishing mortality rate F, we subtracted an assumed value of $M = 0.10$, based on the work of Sainsbury (1982), from the total mortality rate Z. Natural mortality rate is difficult to estimate, especially in fished populations (Shepherd and Breen 1991); Sainsbury used several methods to estimate M in a population protected from fishing. The method of Fournier and Breen (1983) can estimate growth and mortality rates simultaneously but is better applied by constraining the growth estimates, to be consistent with independent estimates. We applied this method to length-frequencies from the northern Marlborough Sounds and D'Urville I., using the growth estimates obtained from mark-recapture data in those regions. This method could not be applied to the other regions because we had no independent estimates of growth.

In using the Fournier and Breen (1983) method, the assumed number of age classes N was determined by examining results using different values of N. We chose the highest value for which the procedure estimated a substantial proportion of the population to be contained within each age-class. At unrealistically high values of N, the procedure estimates that some age-classes are "empty." The parameter NFULL (the index of the first cohort whose abundance is used in estimating mortality) was chosen with reference to the mean cohort length and the minimum legal size. Estimated standard deviations of lengths-at-age around mean length-at-age were constrained to values near 4.1, based on examination of length-frequencies in which cohort modes were clear (Schiel, unpubl. data). L_∞ was unconstrained except for D'Urville I., where a minimum constraint was required to obtain estimates consistent with the mark-recapture data. Population proportions were left unconstrained unless the procedure made unrealistically high estimates for single age-classes. Variance of mean lengths from the von Bertalanffy growth curve and variance of the estimated population proportions from an exponential decay curve were both constrained to a maximum of 1.0. Sensitivity of the procedure to changes in N, NFULL, K, and the standard deviations of length-at-age was examined by varying these parameters (see Tegner et al. 1989).

Modeling

Yield-per-recruit (YPR) modeling was done on a spreadsheet incorporating the YPR model of Ricker (1975). We report results from two regions: the northern Marlborough Sounds and D'Urville I. Length-weight relations were calculated from field sampling results (Table 1). Egg production modeling was done for these regions using a simple spreadsheet model of the form described by Sluczanowski (1984, 1986). The additional information required for this modeling is the length-fecundity relation. Relevant data are available from Poore (1973), Sainsbury (1982), and Wilson (1987). Based on the size range of paua in each of these sources, we used Wilson's data to derive

$$\text{Eggs} = (9.32 \times 10^{-12}) \times \text{shell length (mm)}^{8.408}.$$

The natural mortality rate M was assumed to be 0.10. We assessed the sensitivity of the results to this assumption by varying M. For the northern Marlborough Sounds, we also varied M and the size-at-first-capture and developed the response surface of YPR

Table 1
Length-weight power curves for each of the regions of New Zealand examined. The relation is whole weight (g) = a × (length (mm)^b).

Region	*n*	a	b
Karori Rock	278	3.593E-5	3.305
Stewart I. West	495	5.308E-5	3.169
Stewart I. North	416	3.918E-6	3.718
Stewart I. East	499	2.994E-5	3.303
Marlborough D'Urville	335	2.592E-5	3.322
Marlborough North	497	2.470E-5	3.339
Marlborough South	181	4.927E-5	3.190

and egg production. For each region, the von Bertalanffy growth curves from mark-recapture data were used.

We held the age-at-first-capture constant at the first age-class with a mean length equal to or greater than 125 mm. Then we varied the instantaneous rate of fishing mortality, F, to estimate $F_{0.1}$ and $F_{25\%}$. $F_{0.1}$ is the fishing mortality rate at the point where yield-per-recruit increases with F one-tenth as fast as it does at the origin. Although arbitrary, $F_{0.1}$ is used by several major international stock assessment agencies as a guide to appropriate target fishing mortalities (Mace 1988). $F_{25\%}$ is the fishing mortality rate at which equilibrium egg production is 25% that of an equilibrium virgin population.

Results

Field sampling

Haliotis iris were abundant at all sites, despite more than 30 years of commercial fishing activity in all regions. It was not our intention to estimate densities, but an indication of abundance is given by the length of time it took to obtain our samples. The mean was 155 paua per diver-hour (SD 33.6) or about 32 kg whole wt per diver-hour.

The structure of paua populations varied considerably among the seven regions (Fig. 3). The three regions of Stewart I. show clear differences in the modes (Fig. 3A–C). The west coast region had the major mode at 140–145 mm shell length, well beyond the minimum legal size of 125 mm, and paua were found up to 187 mm. The major mode for the northern region was at 125–130 mm. The east coast region had a higher proportion of smaller paua and the major mode was at 120 mm.

In contrast to Stewart I., length-frequencies for the three regions of the Marlborough Sounds were similar to one another (Fig. 3D–F). The major modes were around 125 mm (MLS), and smaller paua were found in each region. There has probably been roughly similar fishing pressure in these three regions in recent times.

Although the Karori Rock site is closed to commercial activity, it is subjected to considerable illegal fishing (Schiel 1989). The major mode in length-frequency is at 130 mm (Fig. 3G). Because illegal fishing removes paua of all sizes, it reduces paua densities but does not necessarily change the population size structure.

Ageing and growth

A typical ring-count frequency is shown for the Marlborough Sounds D'Urville I. region (Fig. 4). Paua appear to be fully recruited to the sampling procedure by 'age' 10. The greatest ring count we observed was 34 at the west coast of Stewart Island. Growth rates were obtained from the ring count data for all sites (Table 2). Growth parameters from ring-count data and mark-recapture experimental data for two regions (Table 3) and the mean increments predicted from the two methods (Fig. 5) were compared. A large difference between the two methods was evident: the mark-recapture data resulted in higher K estimates and larger L_∞ estimates; estimated growth from mark-recapture data was much greater than from ring-count data. This pattern is the converse of what would be expected if the tagging procedure had retarded growth; therefore, we consider the mark-recapture data to be more reliable. The mark-recapture data are inconsistent with the assumption that one, or even two, rings are laid down annually.

Mortality estimation

Total mortality rates from the catch-curve analyses ranged from $Z = 0.216 - 0.425$ (Table 4). Mortality estimates based on the length-frequency analysis, and the parameters used to obtain them, are shown in Table 5. The estimates varied when N, NFULL, K, and the standard deviation constraints were varied; the pattern of change was not consistent between data sets. Only variation in N caused large variation in estimated Z. The Methods describe an objective procedure for choosing N. The 'best' estimates (using the criteria described above) were $Z = 0.495$ and $Z = 0.507$ for the northern Marlborough Sounds and D'Urville regions, respectively. The extreme range observed over all parameter variations in the two data sets was $Z = 0.238 - 0.995$.

Modeling

Growth rates used in modeling were those estimated from mark-recapture data (Table 3) for the northern

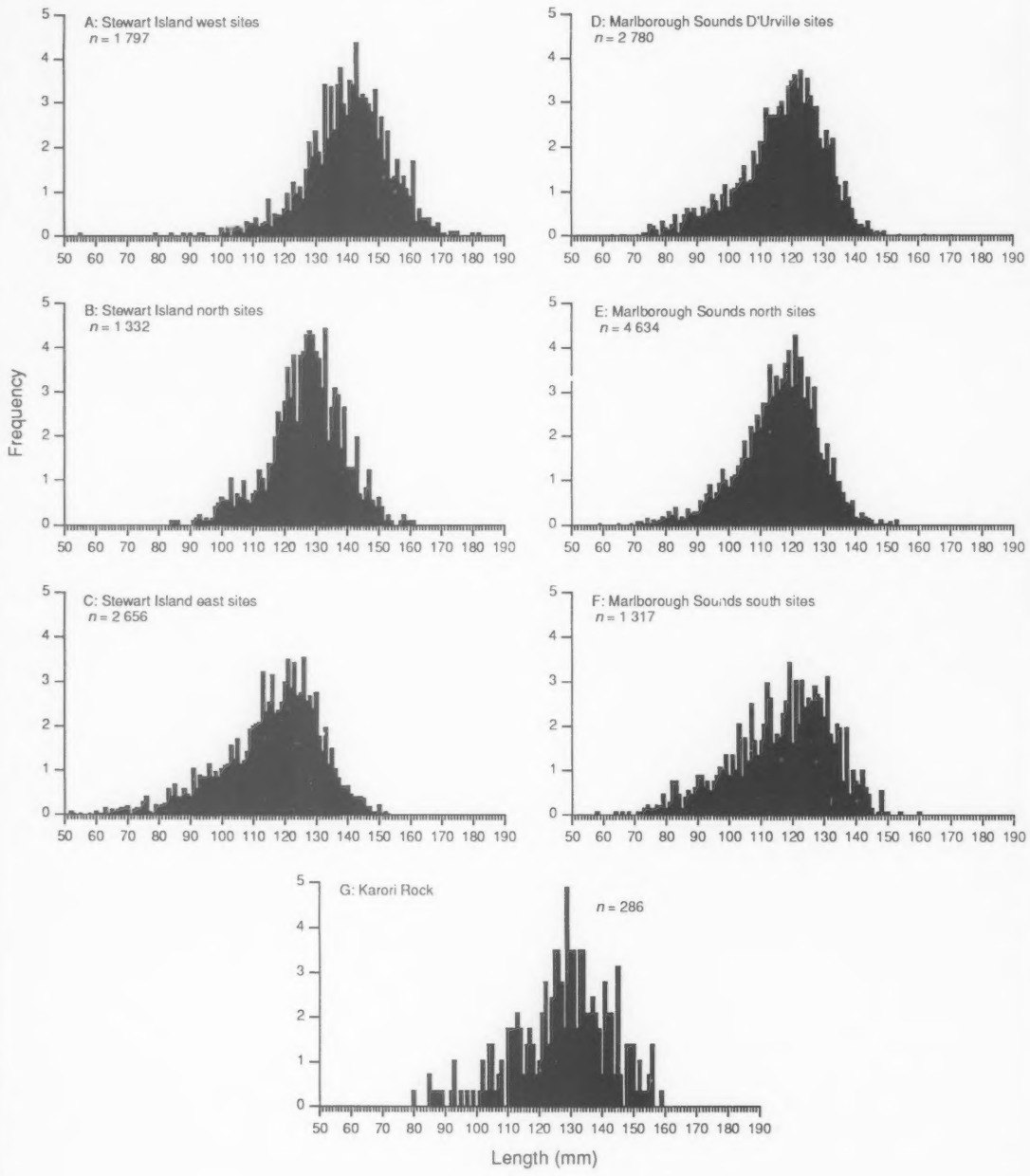

Figure 3
Size-frequency histograms of *Haliotis iris* measured in September and October 1989.

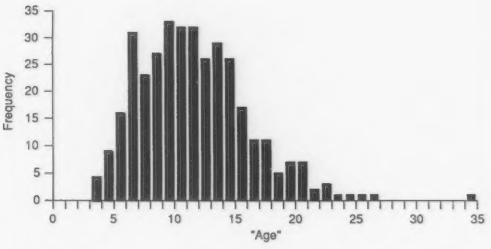

Figure 4

'Age' estimates from growth ring counts (n 335) in one region (Marlborough Sounds D'Urville I.), assuming that one growth ring represents one year of age.

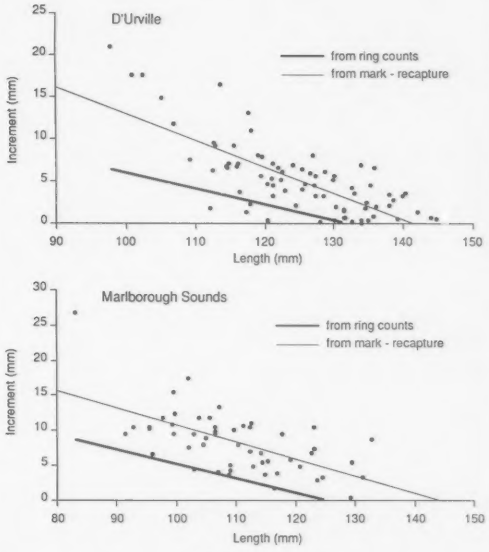

Figure 5

A comparison of the length-specific growth increments predicted from the mark-recapture data (thin line) and from growth ring counts (thick line) in two regions of the Marlborough Sounds. Data points are the observed growth increments; predictions were based on data in Table 3.

Marlborough Sounds and D'Urville I. regions. Growth estimates from ring count data were not used because of the discrepancy seen in Table 3. Estimates of $F_{0.1}$ and $F_{25\%}$ resulting from YPR analyses are given in Table 6 for three assumed M values. In all cases, $F_{25\%}$ was greater than the estimated $F_{0.1}$ obtained from the same parameters.

The best estimates of actual fishing mortality rates, obtained from the procedure shown in Table 5, were substantially higher than $F_{0.1}$ in both regions examined (Table 6). This result is not sensitive to the assumed M, although higher M values increase $F_{0.1}$ and decrease the estimated current level of F. Response surfaces in YPR and egg production resulting from variation in M and the size-at-first capture are shown in Figures 6 and 7, respectively. These show the typical form of such surfaces (cf. Tegner et al. 1989). When M is higher, maximum YPR is obtained at a lower size for a given F, or at a higher F for a given size. Egg production follows a simpler pattern, but is greater at a given combination of F and size-at-first-capture when M is greater. Yield and egg production resulting from different values of M and MLS are shown in Table 7.

Table 2

Estimates of von Bertalanffy growth parameters (with standard errors) from the growth ring-count data of *Haliotis iris* where L_∞ is the asymptotic length, K is the Brody coefficient (Ricker 1975), and t_0 is the theoretical age at length zero.

Region	n	L_∞	K	t_0
Karori Rock	278	143.2 (2.41)	0.160 (0.022)	−8.4 (0.96)
Stewart I. West	495	153.3 (1.63)	0.143 (0.017)	−7.0 (1.17)
Stewart I. North	416	134.1 (0.81)	0.318 (0.034)	−5.9 (0.54)
Stewart I. East	499	130.9 (1.21)	0.283 (0.027)	−6.0 (0.43)
Marlborough D'Urville	335	131.1 (1.79)	0.210 (0.022)	−6.6 (0.53)
Marlborough North	497	135.0 (3.06)	0.114 (0.018)	−11.5 (1.47)
Marlborough South	181	134.8 (2.68)	0.291 (0.042)	−4.7 (0.51)

Table 3

A comparison of von Bertalanffy growth parameters estimated from growth ring-count data from several sites in the D'Urville I. and northern Marlborough Sounds regions (Fig. 1) and mark-recapture data from experiments at the same sites (Talbot Murray, unpubl. data). Sample sizes are unequal because more animals were subjected to ring counting than marks were recovered.

	Mark-recapture data			Ring-count data		
Place	n	L_∞	K	n	L_∞ (SE)	K (SE)
D'Urville I.	79	141.6	0.379	131	131.5 (2.21)	0.197 (0.029)
Northern Marlborough	53	144.5	0.285	180	126.4 (2.65)	0.214 (0.052)

Discussion

Size structure

Evidence from length-frequencies indicates that in some regions the fishery may still be sustained by the accumulated stock. Although reliable catch-per-unit-effort figures are not available for the commercial fishery, it is probable that the west coast of Stewart I. represents such a region. The weather and sea conditions render this region inaccessible for much of the year, but it is a favored place to fish when conditions permit because of the large sizes and abundance of paua. In contrast, sites on the east coast of Stewart I. are considerably more sheltered, generally accessible to fishing, and closer to a port. The observed population structure in the eastern region, with most paua below MLS, is consistent with a population in equilibrium with the fishery.

There are alternative explanations for the differences in size-frequencies. One possibility is a difference in growth rates among regions: L_∞ could be smaller in the eastern region of Stewart I. than the western region. Another possibility is that the population structure seen at the west coast of Stewart I. may have resulted from a short period of good recruitment followed by poor recruitment. A third possibility is that natural mortality is much higher in the eastern region of Stewart than in the other regions. Similarly, population size structures seen in the Marlborough Sounds could be explained by high natural mortality, recruitment variation, or stunted growth in some regions. Only repeated

Table 4

Total mortality estimates, and their standard errors, from the catch curve method, based on growth ring-count data. Sample sizes are given for the ring-count and length-frequency samples.

Region	Ring-count sample	Length sample	Z (SE)
Karori Rock	285	285	0.16 (0.022)
Stewart I. West	319	1796	0.13 (0.017)
Stewart I. North	412	1332	0.19 (0.022)
Stewart I. East	313	2662	0.28 (0.031)
Marlborough D'Urville	173	2780	0.38 (0.049)
Marlborough North	263	4634	0.36 (0.060)
Marlborough South	90	1317	0.25 (0.050)
Total	1855	14806	

Table 5

Estimates of total mortality rate Z based on length-frequencies, using the method of Fournier and Breen (1983). N is the assumed number of age classes; NFULL is the number of the first age-class included in the mortality estimate; "SDevs" are the standard deviations of lengths in the first and last age-classes; T is the value of the objective function minimized by the procedure. Asterisks indicate constrained values.

Region	N	NFULL	SDevs		L_∞	K	T	Z
Northern Marlborough Sounds	14	7	4.1*	4.2*	144.4	0.28*	92.8	0.49
D'Urville I.	12	6	4.2*	4.2*	138.0	0.37*	162.0	0.51

Table 6

Comparison of estimated fishing mortality rates (F) with the reference levels $F_{0.1}$ and $F_{25\%}$ for two regions, and sensitivity of the estimates to assumed natural mortality rate M.

Region	$F_{0.1}$	$F_{25\%}$	Est. F
Northern Marlborough Sounds			
M = 0.05	0.11	0.16	0.45
M = 0.10	0.18	0.27	0.40
M = 0.15	0.25	0.47	0.35
D'Urville I.			
M = 0.05	0.11	0.18	0.46
M = 0.10	0.18	0.32	0.41
M = 0.15	0.27	1.11	0.36

Table 7

Northern Marlborough Sounds region: YPR (top) and egg production (bottom) for three different levels of assumed M, for three different minimum legal sizes. YPR is in grams whole weight; egg production is expressed as a percentage of the eggs produced by a virgin population.

MLS	115		125		130	
M	F_{est}	$F_{0.1}$	F_{est}	$F_{0.1}$	F_{est}	$F_{0.1}$
0.05	219.0	196.1	230.6	199.0	236.5	205.4
0.10	175.9	151.1	176.2	151.1	171.9	147.0
0.15	139.0	126.3	132.5	122.2	122.9	114.4
0.05	7.4	33.4	9.9	35.0	12.8	34.1
0.10	14.0	31.1	18.1	33.3	12.5	36.6
0.15	22.6	31.1	28.2	34.6	33.9	39.1

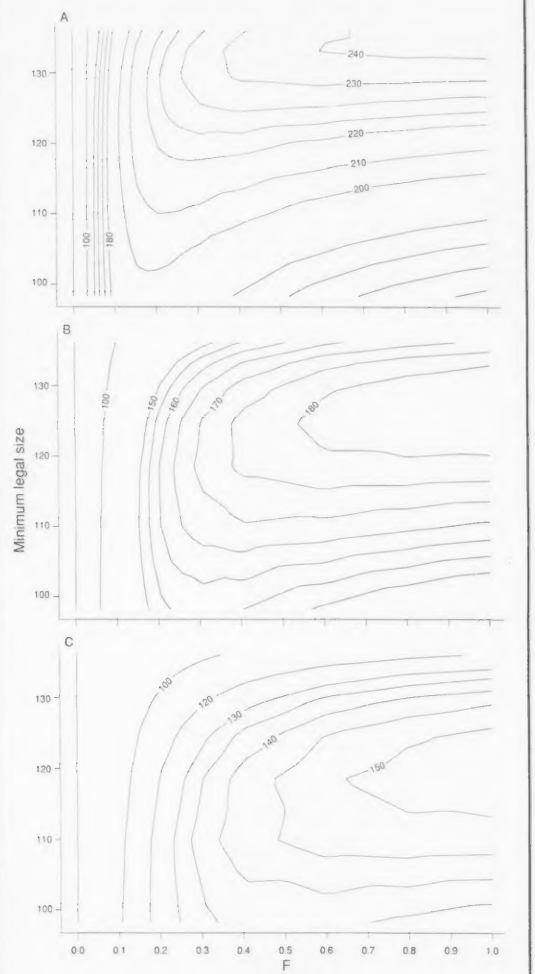

Figure 6
Yield-per-recruit as a function of the natural mortality rate (M), fishing mortality rate (F), and the minimum legal size. In A, M = 0.05; B, M = 0.1; C, M = 0.15.

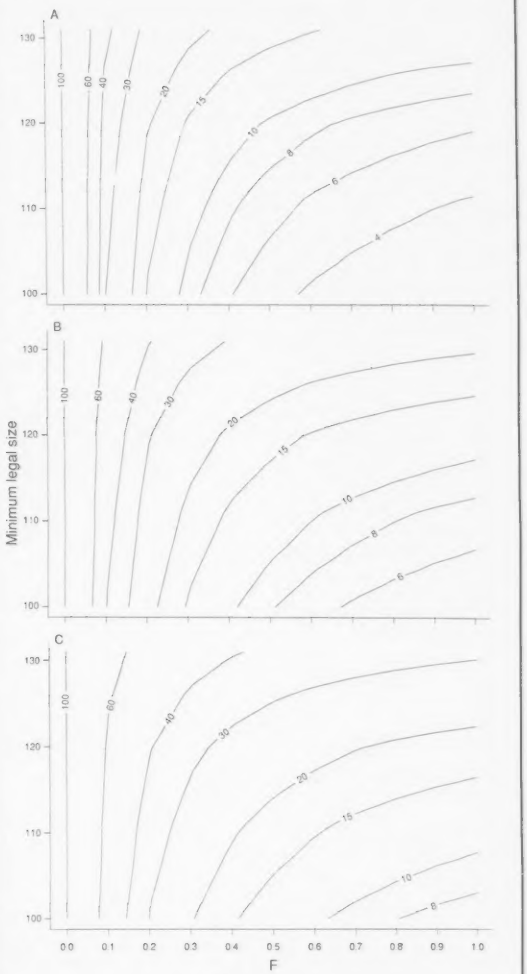

Figure 7
Egg production as a function of the natural mortality rate (M), fishing mortality rate (F), and the minimum legal size. In A, M = 0.05; B, M = 0.1; C, M = 0.15.

sampling through time, and appropriate experimentation, can distinguish among these alternatives.

Ageing and growth

Despite the fact that growth rings in *H. iris* are quite distinct, as has been reported for other species (Prince et al. 1988), they are evidently not annual in at least some populations. Predicted growth increments from ring count data were much less than observed increments from mark-recapture. This suggests that more than one ring is laid down annually, but it is not clear whether the deposition of growth rings follows a regular annual pattern. We examined the hypothesis that the growth rings are semi-annual, but predicted and observed growth increments still did not agree. Consequently, the ring counts overestimate age in two study regions. This appears to be borne out by length-frequency analysis of mortality in which the estimates are higher than those from catch curves.

Our experience underscores the need to validate age estimates from independent data (Beamish and McFarlane 1983). For *H. iris*, the use of growth rings leads to the erroneous conclusion in at least two populations that they are more lightly fished than indicated by length-frequency analysis based on mark-recapture data.

Mortality

For the reasons discussed above, we consider that the mortality rates based on ring counts are spurious for *H. iris*, at least for the regions examined. Mortality rates derived from length-frequency distributions are heavily dependent on the assumptions of the method. One critical assumption is that recruitment to the population is roughly constant. If recent recruitment has varied with any trend, analysis of a single length-frequency sample cannot provide a realistic estimate of mortality (Shepherd and Breen 1991). We have no data on annual variation of recruitment at our sampling sites. Interannual variation can be high in some species of abalone (Tegner et al. 1989), but it is systematic change in recent recruitment that causes estimates to be dubious. However, it is encouraging that our estimates of mortality are reasonably robust to variation in the input parameters (Table 5).

Other important assumptions are that natural mortality is age-independent (over the age range examined) and also constant for all areas. For abalones generally, the first assumption is not unreasonable for mature animals (Shepherd and Breen 1991) and, for *H. iris*, it is consistent with the conclusions of Sainsbury (1982). Our estimates of current fishing mortality rates are sensitive to the assumption that $M = 0.10$ (Table 6). This is the best estimate of natural mortality derived by Sainsbury (1982).

Modeling and implications for management

Of the two reference points we use for evaluating fishing mortality rate in the *H. iris* fishery, $F_{0.1}$ is smaller than $F_{25\%}$ for both regions. This result is insensitive to the assumed M and indicates that $F_{0.1}$ management is more conservative than $F_{25\%}$ management.

The estimated current fishing mortality rates for both regions are greater than both reference levels of F; this result is also insensitive to the assumed value of M. If the underlying assumptions hold, therefore, the current fishery is more intense than can be sustained in the long term in these regions. Egg production at the estimated present level of fishing mortality is about 18% (Table 7). This is lower than prudent management would probably require.

Both reference points are sensitive to several assumptions, similar to those discussed above: random recruitment variation, constant age-independent M, constant growth rates, and the assumed value of M (reviewed by Hancock 1979, Vetter 1988, Breen 1991).

The impact of varying the minimum legal size appears small in comparison with the sensitivity of YPR and egg production analysis to M (Table 7). Neither YPR nor egg production at equilibrium would be affected much by changing the MLS, at least over the range examined. Maximizing YPR by adjusting the MLS would require a much more precise knowledge of M. YPR is robust to changes in F, but decreasing F to the reference level $F_{0.1}$ would increase equilibrium egg production; this would be true whatever combination of M and MLS is examined. This result is similar to that reported by Sluczanowski (1984, 1986) for Southern Australian abalones. He found that egg production could be increased markedly with little sacrifice in YPR in the fishery.

Because of the ease with which paua can be found in most sites, there is a temptation to assume that stocks are healthy and in no imminent danger of overfishing. However, based on our estimates of fishing mortality rates, the recent fishery may be simply removing an abundant accumulated stock at a rate greater than annual production in two study regions.

Our best estimates of fishing mortality rates are higher than the standard reference levels, indicating that fishing pressure should be reduced in these regions. Under an ITQ management regime, this can be addressed by reducing quotas in a QMA. Translating reductions in fishing mortality to reductions in TACCs for Quota Management Areas can be done by evaluating the Baranov catch equations (Ricker 1975). Another approach is to estimate maximum constant yields from historical catch data (Schiel 1989).

Acknowledgments

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Experimental Analysis of Habitat Quality for Juvenile Queen Conch in Seagrass Meadows

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Abstract.—Transplants of juvenile queen conch *Strombus gigas* L. were conducted in the southern Exuma Cays, Bahamas, to test the relationship between large-scale patterns of distribution and differential habitat quality (as indicated by conch mortality and growth). One-year-old conch (mean shell length 93 mm) were transplanted to two locations within known conch nursery habitats, one with low and one with moderate seagrass biomass. Transplants were also made to six sites without resident conch: two sites similar to the moderate biomass site, two sites similar to the low biomass site, one site with heavy seagrass, and one on bare sand.

Mortality was low at stations with natural conch populations and/or moderate seagrass biomass. Mortality was high at all other sites, and increased with time at the sand site and at one of the low biomass sites. Growth rate was high and relatively constant through the experiment at the stations with natural conch populations and at one site with moderate seagrass biomass and no resident conch (C2). Rapidly declining growth rates were found at all other sites despite depth, sediment, and macrophyte characterisitics similar to sites with resident conch. Data on standing crops of macrodetritus at the beginning and end of the experiment indicated food limitation at one site where growth was low. Until the distribution of queen conch is understood, small-scale transplanting will provide a useful tool for evaluating distributional mechanisms and a test for habitats proposed for stock enhancement.

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Seagrass meadows are important nursery habitats for many fishes and invertebrates from high to low latitudes (Thayer et al. 1975, Kikuchi and Peres 1977, Weinstein and Heck 1979, Stoner 1983, Pollard 1984, Robblee and Zieman 1984, Sogard et al. 1987). The queen conch *Strombus gigas* L. is a large gastropod mollusc (to >250 mm shell length) which uses the seagrass habitat as a nursery (Randall 1964, Weil and Laughlin 1984, Stoner and Waite 1990). Food value makes the queen conch an important commercial species throughout the Caribbean region (Brownell and Stevely 1981, Berg and Olsen 1989).

Hatchery data suggest that pelagic larvae of the queen conch spend 18 to 40 days in the water column (Brownell 1977, Davis et al. 1987, Mianmanus 1988). The larvae settle and metamorphose in the benthos and live for the first several months in places and in ways mostly unknown at this time. Juveniles are usually 35–40 mm shell length when first observed on sandy shoals and in shallow seagrass meadows (Stoner and Sandt, unpubl. data). Primary foods for juvenile stages are seagrass detritus and algae (Stoner 1989a, Stoner and Waite 1991). In seagrass beds of the Bahama, Turks, and Caicos Is., Virgin Is., Cuba, and Venezuela, juvenile queen conch densities of 1 to 2 animals/m^2 are common (Alcolado 1976, Hesse 1979, Weil and Laughlin 1984, Iversen et al. 1987, Stoner 1989a). Recent investigations in the Bahamas show that highest densities of juvenile queen conch are associated with seagrass beds of intermediate shoot density (Stoner and Waite 1990). Older juveniles move to deeper water (Weil and Laughlin 1984), and sexual maturity is attained at approximately 3.5 to 4.0 years (Randall 1964, Appeldoorn 1988).

Large seagrass habitats (hundreds of hectares) are found near Lee Stocking I., in the Exuma Cays, Bahamas. Much of this habitat appears to be appropriate for juvenile queen conch (depth, sediments, macrophyte cover); however, conch are associated with certain geographic areas within the seagrass meadows. Five discrete juvenile populations have been observed in particular localities near Lee Stocking I. from 1984 to the present (Wicklund et al. 1988, Stoner, unpubl. data).

Reported here are the results of experimental transplants designed to examine qualities of seagrass meadows which provide optimal habitat for juvenile queen conch. The following two hypotheses were tested using conch survivorship and growth as indicators of habitat quality: (1) habitat quality is directly related to seagrass biomass; and (2) Habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch.

Site description

Experiments with juvenile queen conch were conducted during the summer of 1988, at eight sites in the southern Exuma Cays, Bahamas, near Lee Stocking I. (Fig. 1). These sites included two which have natural populations of queen conch juveniles, Children's Bay Cay site 1 (C1) and Neighbor Cay site 1 (N1). Site C1 had moderate turtlegrass *Thalassia testudinum* biomass, and N1 had low biomass (Fig. 2). Site N1 had lower seagrass biomass than the optimal for juvenile conch reported by Stoner and Waite (1990) but has had a persistent population of conch since at least 1986. Two sites were chosen with macrophyte, sediment, and depth characteristics similar to C1, but with no resident conch populations. Children's Bay Cay site 2 (C2) was in the same seagrass bed as C1 but 0.5 km to the southeast; the other site was west of Lee Stocking I. (L1). An additional two sites were chosen for similarity to N1: one site was north of Lee Stocking I. (L3) and the second near Windsock Cay (W1).

To examine the effects of seagrass biomass in extreme cases, two additional sites were chosen. A sand bank site, Children's Bay Cay site 3 (C3), was selected where there was no macrophyte cover but which has a regular transience of juvenile conch. One additional site, Lee Stocking I. site 2 (L2), was chosen for high seagrass and detrital biomass, 300 m northwest of L1.

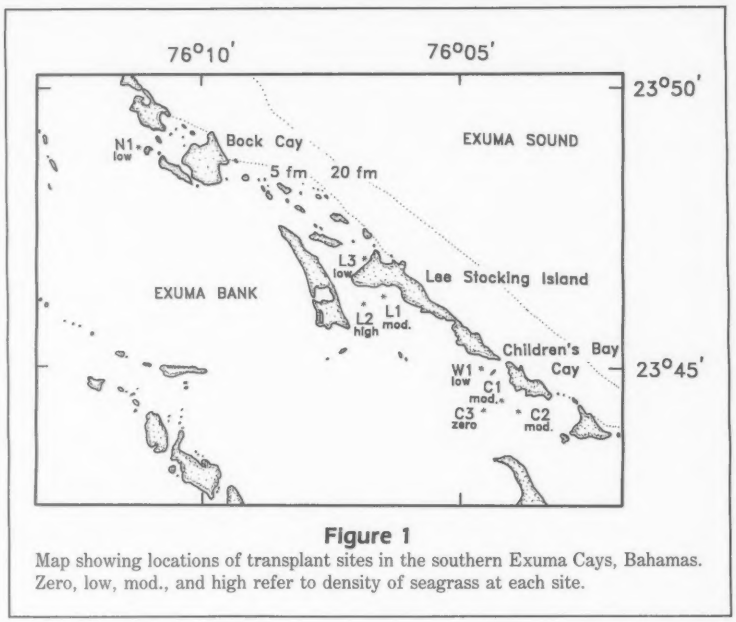

Figure 1

Map showing locations of transplant sites in the southern Exuma Cays, Bahamas. Zero, low, mod., and high refer to density of seagrass at each site.

Methods and materials

Two topless cages were constructed at the eight experimental sites with 2.0 cm black plastic mesh wired to reinforcement bar driven into the sediment. The

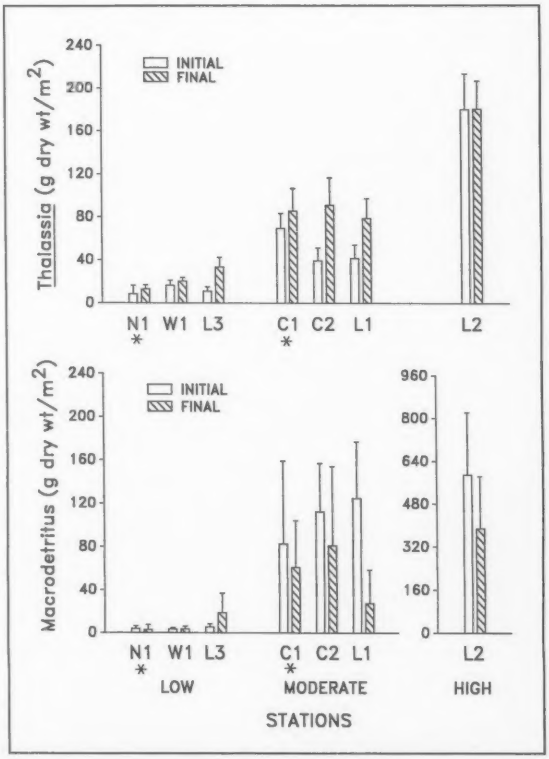

Figure 2

Standing crop of *Thalassia testudinum* and macrodetritus at sites where juvenile queen conch were transplanted. Histograms are mean values found in enclosures at the beginning and end of the experiment. Error bars are ± standard deviation. Note the change of scale for macrodetritus at station L2. Asterisks indicate stations with resident conch. Station C3 (not shown) had zero macrophyte biomass.

Table 1

Habitat characteristics of eight sites where juvenile queen conch were transplanted. Depth is the mean at low water. Values for sediments are mean ± standard deviation (n 2). Asterisks and plus signs indicate mean values which are not different statistically (ANOVA and Neuman-Keuls test; $P<0.05$).

Site	Resident conch	Seagrass biomass	Depth (m)	Sediment grain-size (ϕ)	Sediment sorting (ϕ)	Sediment organics (%)
C3	No	Zero	1.3	1.50±0.02*	0.84±0.10*	2.38±0.33+
N1	Yes	Low	2.3	1.52±0.10*	1.14±0.06*	2.68±0.14*+
L3	No	Low	2.2	2.02±0.30*	1.08±0.20*	3.66±0.33*
W1	No	Low	2.0	1.82±0.20*	1.47±0.28*	3.83±0.47*
C1	Yes	Moderate	3.6	2.56±0.29*	1.39±0.22*	3.76±0.33*
C2	No	Moderate	3.7	1.15±0.11*	1.62±0.19*	2.80±0.33*+
L1	No	Moderate	3.4	2.26±0.23*	1.40±0.23*	2.92±0.32*+
L2	No	High	3.7	2.40±0.19*	1.04±0.07*	5.36±0.48

cages were 30 cm high, 5 m in diameter, and pushed into the sediment approximately 2.0 cm to prevent loss of animals. Exact positions of the cages were chosen to provide uniformity in macrophyte cover at each site, and to insure that sites selected for similar characteristics (C1, C2, L1 and N1, L3, W1) had equivalent seagrass and detrital cover as well as sediment quality (Table 1, Fig. 2).

Previous experiments with the same cage design at Children's Bay Cay site 1 showed that the cages did not effect sediment grain-size, sediment chlorophyll, or accumulation of detritus. Enclosed animals had growth rates equivalent to individuals tagged and released in the field surrounding the enclosures (Stoner 1989a).

Animals used in this experiment were 1-year-old *Strombus gigas* collected from the sand bank near Children's Bay Cay. At the beginning of the experiment, all of the conch were between 82 and 105 mm total shell length. Mean lengths in individual treatments were not different at the beginning of the experiment (ANOVA, F 1.90, $P>0.05$), ranging from 92.0 to 94.3 mm. After measuring habitat characteristics (see below) and clearing all noticeable macroinvertebrates from the 16 enclosures, 24 individually tagged and measured conch were placed in each cage (1.2 conch/m^2), yielding a density equivalent to mean summer population density at C1 and N1. Dead or lost conch were replaced to maintain the population density within cages (Table 2). Replacements were of a size similar to the mean conch size in a particular treatment at the replacement time. Conch were marked with vinyl spaghetti tags (Floy Tag & Mfg., Inc.) tied around the shell spire.

All transplants were made by 26 April 1988, and measurements of total shell length (spire to siphonal canal) were taken with calipers at 35, 75, and 120 days. Growth rate was determined on the basis of mm shell growth per day. Each enclosure was examined at approximately 2-week intervals to determine mortality rates over time, to replace dead conch, and to remove invading invertebrates. One of the cages at C3 was destroyed by wave action in June 1988, and all of the enclosed animals were lost. This cage was rebuilt and new animals were introduced on 23 June.

At the end of the experiment, soft tissue weight of individual conch was determined by drawing the animal from its shell after freezing and subsequent thawing. Wet weight was measured after washing away feces and light blotting of the tissues. Body condition was determined by the ratio of wet weight:shell length.

Living macrophytes and macroscopic detritus were collected from each enclosure at the beginning and end of the experiment. Four replicates were taken from 25×25 cm quadrats into nylon bags (3.0 mm mesh) for determination of aboveground biomass. Individual samples were divided into green *Thalassia testudinum* blades and detritus (senescent blades and blade fragments). The only other macrophytes collected were the seagrasses *Syringodium filiforme* and *Halodule wrightii* found in very small amounts, and an occasional calcareous green alga *Rhipocephalus phoenix*. The aboveground fractions were dried at 80°C to constant weight. *Rhipocephalus phoenix* was not included in analysis of macrophytes because of the large bias created in dry weight and because the alga is not consumed by juvenile conch.

Sediments to 5 cm depth were sampled with a 3.5 cm diameter core tube, one sample per enclosure. These samples were frozen until laboratory analyses were performed. Sediment organic content was determined by drying a subsample of approximately 50 g wet

Table 2

Summary of replacements made for loss or mortality of juvenile queen conch in enclosures, by date, site, and cage number. Twenty-four animals were maintained per cage, 26 April–25 August 1988.

Site	Cage	Resident conch	Seagrass biomass	11 May	31 May	21 June	11 July	1 August	Total
C3	1	No	Zero	1	2	5	1	Terminated	9
	2	No	Zero	1	0	5	4	Terminated	10
N1	1	Yes	Low	0	0	0	0	0	0
	2	Yes	Low	0	0	0	0	0	0
L3	1	No	Low	4	2	11	3	11	31
	2	No	Low	1	9	3	4	1	18
W1	1	No	Low	0	0	1	0	0	1
	2	No	Low	0	0	3	8	20	31
C1	1	Yes	Moderate	0	0	0	0	0	0
	2	Yes	Moderate	0	0	0	0	0	0
C2	1	No	Moderate	1	0	2	0	1	4
	2*	No	Moderate	1	3	1	0	0	5
L1	1	No	Moderate	0	4	4	0	2	10
	2	No	Moderate	2	4	0	0	2	8
L2	1	No	High	6	7	9	3	1	26
	2	No	High	2	4	5	6	4	21

*This cage was rebuilt and all animals were replaced on 23 June 1988.

weight at 80°C to constant weight and incineration at 500°C for 4 hours. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another subsample of approximately 50 g was analyzed for granulometric properties. The sample was washed to remove salts and to extract the silt-clay fraction (<62 μm) which was analyzed with standard pipette procedures (Galehouse 1971). The sand fraction (>62 μm) was analyzed with standard sieve fractionation procedures (Folk 1966). Product-moment statistics were generated for mean grain-size and sortedness (McBride 1971).

Analysis-of-variance techniques were applied according to Sokal and Rohlf (1969), with $\log_{10}$ transformations where Bartlett's test indicated heterogeneity of variances (macrophyte data). Conch growth data proved to be heterogeneous in variance in most cases, as indicated by Bartlett's test and plots of means versus variances. Heterogeneity was improved little by log-transformation. Additionally, necessary replacement of conch during the transplant experiment produced a violation in independence in the growth data. For these reasons, Kruskal-Wallis analysis of variance was followed by nonparametric Mann-Whitney U-tests for multiple comparison of growth rates.

Results

Changes in habitat characteristics

Juvenile conch were transplanted to four different habitat types based upon macrophyte biomass: zero, low-, moderate-, and high-biomass habitats (Table 1). Sediment grain-size varied from 1.15 to 2.56 ϕ at the eight sites; however, there were no significant differences in mean values (ANOVA, F 2.26, $P>0.05$), and all are classified as fine to medium sand. Similarly, there were no differences in sediment sorting coefficients (F 2.09, $P>0.05$), with all sites except the bare sand (C3) in the poorly sorted range. Significant differences occurred in sediment organic content (F 15.97, $P<0.001$) with highest values at the high-biomass site (L2) and lowest at the sand site (Table 1). There were no significant differences in sediment organics among the sites with low or moderate biomass.

At the beginning of the experiment there were no significant differences in biomass of either seagrass or macrodetritus between the two cages at any site (Student's t-test, $P>0.05$). Analysis of variance indicated that macrodetritus varied significantly (F 76.48, $P<0.001$) among the eight sites, but there were no significant differences in mean values for the three low-biomass stations (N1, L3, W1) or for the three moderate biomass sites (C1, C2, L1) (Neuman-Keuls test, $P>0.05$). Macrodetritus was more abundant at the

high-biomass site (L2) than at any other site ($P<0.05$), and zero at the sand site (C3) (Fig. 2). The same pattern occurred with living seagrass biomass, except that site C1 had significantly higher biomass than the other moderate-biomass sites, but less than that found at the high-biomass location (L2) (ANOVA, F 58.12, $P<0.001$; Neuman-Keuls test, $P<0.05$).

For analysis of seagrass and macrodetritus standing crops at the beginning and end of the experiment, paired-comparison analysis of variance was conducted, where differences between cages and the effect of time were examined. Significant difference between cages occurred only at N1 where enclosure 2 had a higher biomass of living seagrass than enclosure 1 (F 7.46, $P<0.05$). Paired cages had similar amounts of macrodetritus at all sites ($P>0.05$). Significant differences with time were found at L1 where detritus decreased (F 13.22, $P<0.005$), while living seagrass increased with time (F 20.15, $P<0.001$). Seagrass increased also at C2 (F 23.12, $P<0.001$) and at L3 (F 34.89, $P<0.001$). No other significant time effects occurred for either macrodetritus or seagrass biomass.

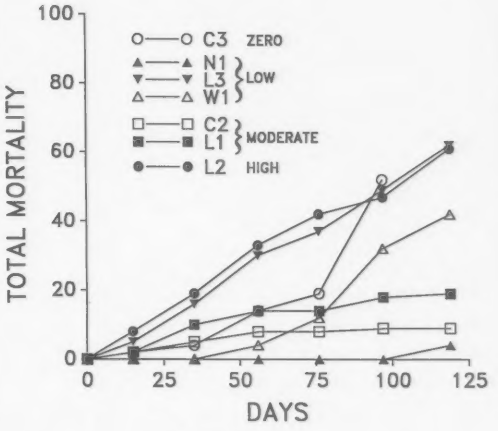

Figure 3
Total mortality of juvenile queen conch shown as a function of time at eight transplant sites near Lee Stocking I. Values are direct counts where 48 conch were transplanted to each site at the beginning of the experiment and replaced upon death. There was zero mortality at station C1 (not shown). Conch were resident at stations C1 and N1.

Mortality

Mortality at experimental sites with natural populations of conch was low, ranging from zero at site C1 to a total of only four individuals during the last three weeks of the experiment at site N1 (Fig. 3). Total mortality at the sites with moderate seagrass density and no resident conch was also low: nine individuals at station C2 and 19 at L1. At both of these sites, mortality rates decreased with time. Mortality was high at all other sites, with either a constant (sites L2 and L3) or accelerating rate (C3 and W1). By the end of the experiment, 61 animals had died at the high-biomass site (L2) and 61 had died at one of the low-biomass sites (L3). At the sand site (C3), the transplant experiment was terminated after 95 days because of rapidly accelerating mortality.

Kruskal-Wallis test was insufficiently powerful to distinguish mortality differences among the sites ($H_{adj.}$ 13.37, P 0.064) despite mortality rates ranging from 0 to 129% of the original number of conch transplanted. This is related to the low number of degrees of freedom in the design (2).

Growth

Growth rates decreased over the three experimental periods at most of the stations, but the decrease was variable among stations, and most extreme at W1 (Fig. 4). Because of station-time interaction in growth rates, Kruskal-Wallis analyses were performed for each growth period to test for station effects. In all cases the effect of site was highly significant ($H_{adj.}$ 164, $P<0.001$ for period 1; $H_{adj.}$ 234, $P<0.001$ for period 2; and $H_{adj.}$ 209, $P<0.001$ for period 3).

During the first growth period, there were no significant differences between growth rates at low-biomass site W1 and moderate biomass site C2 (Mann-Whitney U-test, U 993, P 0.441), between moderate-biomass sites C1 and L1 (U 858, P 0.297), or between sites N1 and L2 (U 825, P 0.572). Growth rates at W1 and C2 were higher than all other sites ($P<0.05$). Rates at sites L3 and C3 were different from all other sites ($P<0.05$). During this period there were no significant differences in growth rates between paired cages ($P>0.05$).

During period 2, growth rates at C1, C2, and N1 were higher than those at the five other stations ($P<0.05$) and different from one another ($P<0.05$). Despite negative growth (shell erosion) at L2 and L3, growth rates at L2, L3, C3, and W1 were not different ($P>0.05$). A significant difference in growth rates between cages at C3 (U 371, P 0.001) was the result of new animals being introduced in the rebuilt cage 1 during this period; however, growth rates were low in both cages.

As in period 2, highest growth rate during period 3 was observed at the moderate-biomass site C2 where there was no resident conch population. Rates at W1,

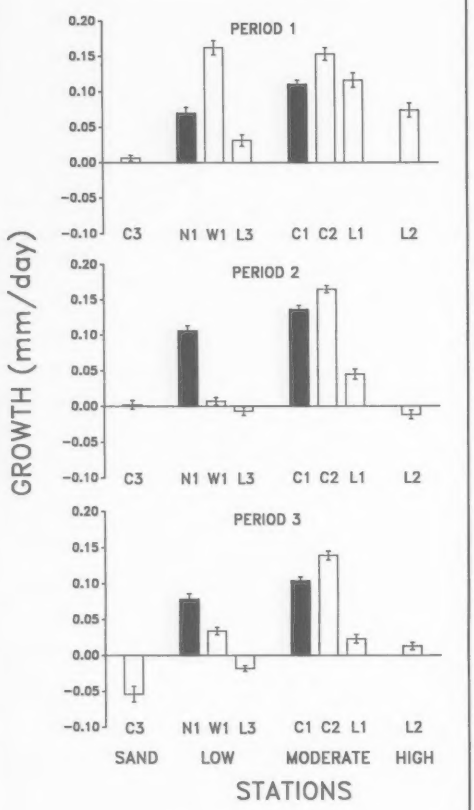

Figure 4
Growth rates for juvenile queen conch at eight transplant sites during three growth periods. Values are mean ± standard deviation. Black bars represent growth rates at sites with resident conch populations. Period 1 = 35 days, Period 2 = 40 days, Period 3 = 45 days.

Table 3
Condition factor of juvenile queen conch transplanted to eight different sites. Values are mean ± standard deviation (n 15). Vertical bars indicate sites for which medians were not different (Mann-Whitney U-tests, $P>0.05$).

Site	Resident conch	Seagrass biomass	Condition factor
C2	No	Moderate	0.257 ± 0.030
C1	Yes	Moderate	0.246 ± 0.031
N1	Yes	Low	0.227 ± 0.031
L2	No	High	0.216 ± 0.036
L1	No	Moderate	0.208 ± 0.025
L3	No	Low	0.188 ± 0.034
W1	No	Low	0.180 ± 0.030
C3	No	Zero	0.165 ± 0.020

L1, and L2 were low and not different $P>0.05$). Growth rates at all other sites were different, and strongly negative growth rates occurred at station C3 and L3. There were no significant cage differences at any of the sites during this period ($P>0.05$).

High growth rates at sites C2 and C1 were associated with high body condition (Table 3). Predictably, condition was low in the bare-sand habitat and other sites where survivorship was low (e.g., L3, W1), and there were various site differences (Kruskal-Wallis test, $H_{adj.}$ 57.38, $P<0.001$) (Table 3). Despite high mortality and low growth rate at the high-biomass site (L2), condition factor at that site was not significantly different from site N1, a natural conch habitat.

Comparing rates of mortality and growth, a pattern emerges: low growth occurred with high mortality at sites C3 and L2. Accelerating mortality and rapidly declining growth rates were found at W1 and L3, while mortality remained low and growth rates high at C1, C2, and N1. At L1, mortality was low but growth declined from a high rate in the first period.

Discussion

Growth rates found in the natural conch habitats (C1 and N1), between 0.1 and 0.2 mm/day, were similar to those determined for free-ranging juveniles at C1 during summer 1985 (0.12 mm/day)(Wicklund et al. 1988), and summer 1987 (0.10–0.15 mm/day)(Stoner 1989a). The rates reported here are also similar to those reported from Los Roques, Venezuela, where growth curves give mean growth rates of 0.16 mm/day for tagged conch between 85 and 105 mm in shell length (Laughlin and Weil 1982), and 0.14 mm/day for 90 mm conch (Brownell 1977). These results suggest that enclosures used in this experiment did not inhibit growth in the test animals.

So that the numbers of conch in the enclosures remained constant, dead conch were replaced with new individuals which, in the less optimal sites, grew at a rate slightly higher than conch enclosed earlier. Replacement, therefore, results in overestimation of growth rate (and probably survivorship) in the poor-quality habitats and conservative separation of sites. Differences in shell length among the experimental sites by the second and third growth periods, and slight differences in growth rates of conch between 90 and 120 mm (Brownell 1977) would have only a minor in-

fluence on site differences. Despite these limitations, high mortality rates and low or negative growth rates provide clear evidence that five of the sites without resident conch (except site C2) were poor habitats for juvenile queen conch.

Stoner and Waite (1990) showed that 1- and 2-year-old conch actively select areas with intermediate seagrass biomass over areas with high and low biomass. Additionally, it was shown that seagrass shoot density and biomass were good predictors of juvenile conch distribution within nursery habitats. Among the sites which were known to serve as natural habitats for queen conch (C1, C3, N1) there was a direct relationship between seagrass biomass and habitat quality, as measured by conch growth. On the larger scale of this study, however, seagrass density was not a good predictor for conch success, and other variables—probably trophic factors—need to be examined.

Adult and subadult queen conch are generally considered to be herbivores (Robertson 1961, Randall 1964, Hesse 1976), but recent data on juvenile conch living in seagrass beds show that seagrass detritus is consumed in large quantities, and macroalgae such as *Batophora oerstedi* and *Laurencia poitei* are primary sources of nutrition (Stoner and Waite 1991). Field experiments have shown that juvenile conch can have a major influence on detritus and other characteristics of the benthic environment, with much of the benthic productivity being removed by grazing (Stoner 1989a,b). The observed depletion of detrital biomass followed by decreasing conch growth rates at the moderate biomass site L1 suggests trophic limitation at that station.

Abundance of macrophytes does not necessarily provide superior habitat. Site L2 had a thick accumulation of detritus and high seagrass biomass, but conch transplanted to that site had high mortality and low growth rates. Randall (1964) noted that young conch may not be able to move readily through dense seagrass stands, and are rarely found in that habitat type.

No attempt is made here to equate mortality rates in the transplants with natural mortality because of potential density-dependent effects on predation rate, partial exclusion of predators by cages, and uncertainty in the sources of mortality. Observations of potential queen conch predators in the enclosures were rare. The tulip snail *Fasciolaria tulipa* was seen attacking conch three different times, and in a few instances the giant hermit crab *Petrochirus diogenes* was found in empty shells; both of these species are known predators on queen conch (Randall 1964, Jory 1982). The apple murex *Murex pomum* and hermit crabs *Paguristes* sp. were observed occasionally in the enclosures, but both are thought to be scavengers (Jory and Iversen 1983, Iversen et al. 1986). Lack of broken shells, low body condition, and low shell growth rates lead us to conclude that much of the mortality in "poor" habitats was a result of inadequate food resources. On the other hand, large differences in mortality rate between the two enclosures at two of the sites suggest that heavy predation may have occurred in some cages.

The fact that one site with no resident juvenile conch (C2) produced high growth rates and survivorship suggests that queen conch do not occupy all suitable habitats. Several explanations are plausible: Pelagic larvae may not be dispersed to the area, settlement may not occur, or early-juvenile stages may suffer high mortality rates at the site. It is also possible that, historically, site C2 has been a nursery site for queen conch. Macroscopic conch shell fragments at the site were found in a density of 3.0 fragments/m^2; this is lower than the density at site C1 (6.8/m^2), but considerably higher than that in other non-conch areas (e.g., density at L1 was 0.05 fragments/m^2) (Stoner and Yoshioka, unpubl. data).

Presence or absence of juvenile queen conch in seagrass meadows appears to be mediated by site-specific characteristics. Habitat quality, as measured by growth rate, was related directly to seagrass biomass in natural conch sites; however, the hypothesis that habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch is clearly rejected. Until the distributional ecology of queen conch is understood, small-scale transplanting will be a valuable tool in manipulations designed to test the significance of other environmental variables, and as a means of testing habitats where enhancement of stocks is proposed.

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Otolith Size versus Weight and Body-Length Relationships for Eleven Fish Species of Baja California, Mexico

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Identification of otoliths recovered from scats or stomachs of marine mammals has been used in feeding-habit studies in recent years (Fitch and Brownell 1968, Brown and Mate 1982, Antonelis et al. 1984, Aurioles et al. 1984). Because of the relatively large number of pinniped scats available, this method has proven useful for identifying prey. However, the method depends on the laborious collection of otoliths from fish in the study area. The relative frequency of a prey species in the diet is determined by the number of otoliths (either right or left) counted. However, two prey species with the same otolith count may not be of equal importance in the diet because of differences in biomass. Antonelis et al. (1984) addressed this problem by estimating the biomass of fish and one species of squid off California, from regressions of weight (biomass) versus the size of otoliths (or squid beaks). The relationship of otolith length to fish size or weight has been reported for other areas (Frost and Lowry 1981, Wyllie Echeverria 1987).

Eleven known species of California sea lion *Zalophus californianus* prey (Aurioles et al. 1984, Lowry and Oliver 1986) were sampled to obtain weight, body length, and otolith length to estimate regressions. These results will be useful for estimating prey size and weight in feeding-habit studies in areas where these fish species occur.

Methods

Fish were sampled by bottom trawling with commercial shrimp nets. Trawls were conducted at depths of 30–200 m on the continental shelf off the Pacific coast of Baja California (23°–27°N lat.) and in the southern Gulf of California. Trawling, fish sampling, and fish measurements were conducted aboard the Research Vessel El Puma owned by the Universidad Nacional Autonoma de Mexico during cruises in the summer and fall of 1987 and the summer of 1988.

Standard length (mm) and weight (g) were recorded for fresh fish specimens. Weight (±0.01 g) was measured using a digital scale (Ohaus). Calipers were used to measure the greatest length (anterior tip to posterior projection) of each dissected sagittal otolith. Values were averaged for each otolith pair. Linear regressions were used to determine the relationship between standard length or fish weight and otolith length.

Results and discussion

Eleven fish species were studied (Table 1). Serrano *Serranus aequidens* and yellowbelly lizardfish *Synodus jenkinsi* were collected in Bahia de La Paz (Golfo de California), while the remaining nine species were typically found off the western coast of Baja California.

The standard length of fishes sampled in this study fell within lengths reported in the literature (Miller and Lea 1976, Eschmeyer et al. 1983) (Table 1). Linear regression of otolith length (mm) against fish length for all species are given in Table 2.

A high correlation coefficient was obtained for the longfin sanddab *Citharichthys xanthostigma* (r 0.974) in spite of the small sample size (Table 2). This was probably due to the relatively large size range of individuals in the sample. Scatter plots of fish length on otolith length for 8 of the 11 species are shown in Figures 1–8. The remaining three species had correlation coefficients smaller than r 0.86 and were not plotted.

The equation for hake (Table 2) was the highest for the sampled species. Antonelis et al. (1984) calculated a regression equation for Pacific hake *Merluccius productus* collected off California. Using an otolith of 6 mm in length in their equation ($Y = 26.2 + 19.38x$), the predicted fish length would be 142.5 mm. Using the equation in Table 2 for hake collected in this study yields a length of 113.76 mm. A "dwarf" Pacific hake in Baja California waters was reported by Vrooman and Paloma (1977). Inada (1981) in an extensive study of the genus stated that the "dwarf" form is actually Panama hake *Merluccius angustimanus*. It is probable that our sample specimens were this species, which is limited in range to the area between 24° and 27°N latitude. According to Vrooman and Paloma (1977), and confirmed by several cruises conducted by the Centro de Investigaciones Biologicas de B.C.S (CIB), the southern limit of distribution of the "large" form of Pacific hake is probably near Bahia Sebastian Vizcaino (28°N lat.).

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Table 1

Lengths and weights of fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Scientific name	Common name*	Maximum standard length (mm)**	n	Ranges of lengths and weights (mm)	(g)
Hippoglossina stomata	Bigmouth sole	400	83	95–230	11.8–240
Lepophidium prorates	Pink cusk eel	—	39	107–223	3.6–62
Ophidion scrippsae	Basketweave cusk eel	280	106	160–242	37.8–115
Serranus aequidens	Serrano	—	43	89–166	13.3–88.5
Prionotus stephanophrys	Lumptail searobin	390	193	67–240	5.6–263
Merluccius angustimanus	Panama hake	910	183	89–220	5.4–103.6
Calamus brachysomus	Pacific porgy	610	36	163–350	141.3–1135.6
Citharichthys xanthostigma	Longfin sanddab	250	46	59–200	1.8–161
Porichthys myriaster	Specklefin midshipman	510	75	140–350	25.7–527.5
Synodus lucioceps	California lizardfish	640	34	160–430	29.4–578
Synodus jenkinsi	Yellowbelly lizardfish	—	41	185–406	46.5–580.2

*Common name assigned in this study.
**Data from Miller and Lea 1976, Eschmeyer et al. 1983.

Table 2

Regression equations for fish length (Y) vs. otolith length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	n	Equation* $Y = a + bX$	Correlation coefficient	Percent r^2
Bigmouth sole	83	$Y = (-5.976) + 5.47X$	0.873	76.26
Pink cusk eel	39	$Y = (-3.103) + 23.76X$	0.915	83.77
Basketweave cusk eel	106	$Y = (3.408) + 29.30X$	0.930	87.86
Serrano	43	$Y = (1.539) + 1.830X$	0.857	73.56
Lumptail searobin	193	$Y = (-17.649) + 27.26X$	0.928	86.22
Panama hake	183	$Y = (13.564) + 16.7X$	0.979	95.89
Pacific porgy	36	$Y = (-10.337) + 4.174X$	0.945	89.31
Longfin sanddab	46	$Y = (-3.898) + 31.48X$	0.974	94.97
Specklefin midshipman	75	$Y = (-4.518) + 2.92X$	0.954	91.05
California lizardfish	34	$Y = (1.694) + 4.975X$	0.821	67.44
Yellowbelly lizardfish	41	$Y = (-2.515) + 5.827X$	0.864	74.78

*$P = 0.01$ for all equations.

Since equations for both the California and the Baja California samples were highly significant, the observed differences cannot be explained by measurement errors or data variation, but probably reflect different hake species.

Fish weight was regressed against otolith and fish lengths (Tables 3 and 4). When otolith size was used to estimate fish weight directly, the correlation coefficient, and consequently percent r-squared for some species (Table 3), was slightly smaller than the respective values of fish weight estimated from fish length (Table 4). Regression lines and scatter plots for eight fish species studied are shown in Figures 1–8.

Coefficients of fish weight on fish length were the highest (Table 4). The value of r^2 was greater than 90% in all cases. Thus, when comparing prey importance based on biomass in feeding-habit studies, both equations (Tables 3 and 4) should be used to estimate weight.

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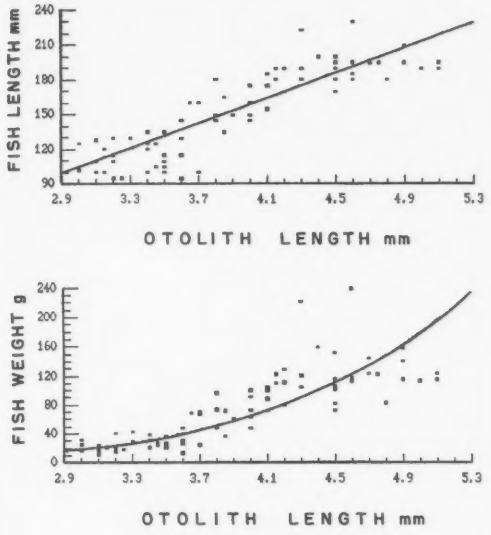

Figure 1
Relationship of fish length and weight to otolith size for bigmouth sole *Hippoglossina stomata* from Baja California.

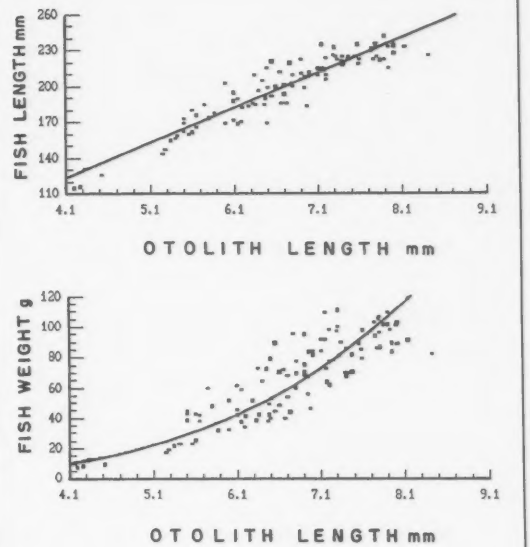

Figure 3
Relationship of fish length and weight to otolith size for basketweave cusk eel *Ophidion scrippsae* from Baja California.

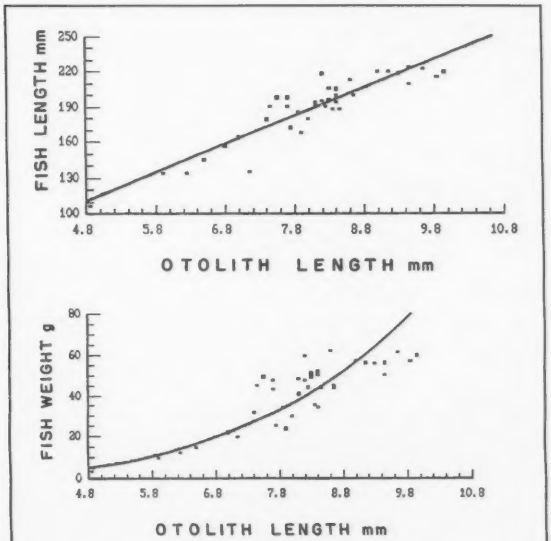

Figure 2
Relationship of fish length and weight to otolith size for pink cusk eel *Lepophidium prorates* from Baja California.

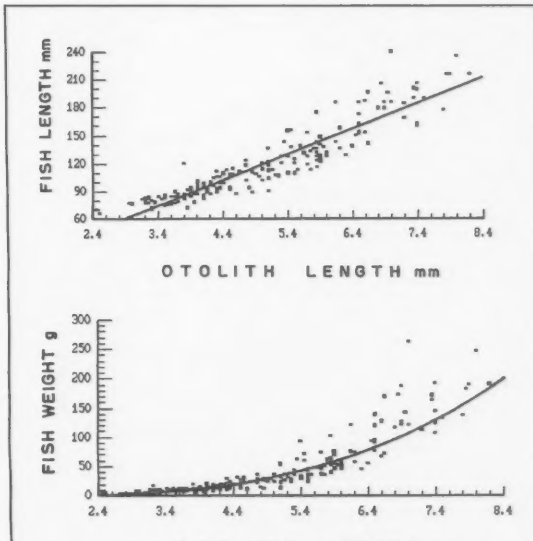

Figure 4
Relationship of fish length and weight to otolith size for lumptail searobin *Prionotus stephanophrys* from Baja California.

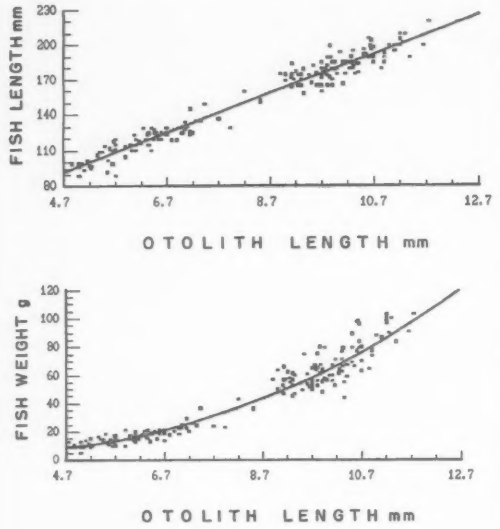

Figure 5
Relationship of fish length and weight to otolith size for Panama hake *Merluccius angustimanus* from Baja California.

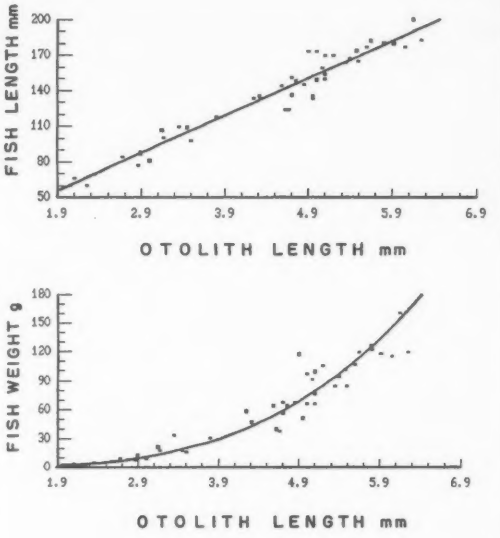

Figure 7
Relationship of fish length and weight to otolith size for longfin sanddab *Citharichthys xanthostigma* from Baja California.

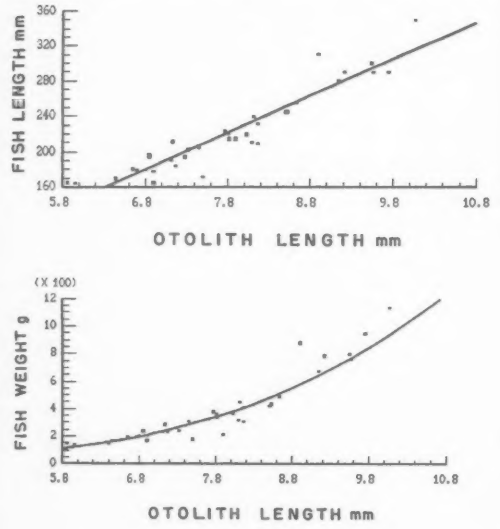

Figure 6
Relationship of fish length and weight to otolith size for Pacific porgy *Calamus brachysomus* from Baja California.

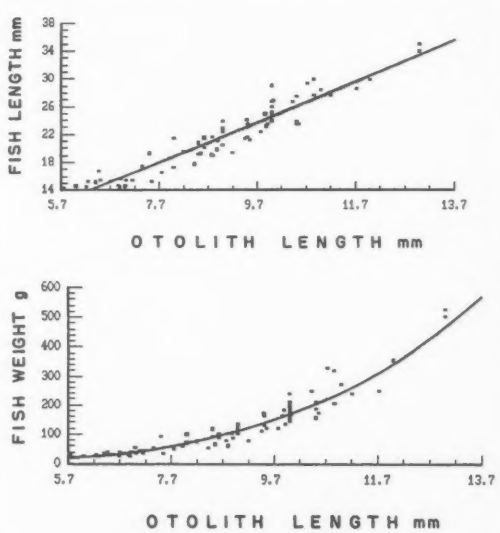

Figure 8
Relationship of fish length and weight to otolith size for specklefin midshipman *Porichthys myriaster* from Baja California.

Table 3

Regression equations for fish weight (Y) vs. otolith length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	Equation* $Y = a X^b$	Correlation coefficient	Percent r^2
Bigmouth sole	$Y = (-2.084) X^{4.51}$	0.877	76.93
Pink cusk eel	$Y = (-4.222) X^{3.75}$	0.912	83.20
Basketweave cusk eel	$Y = (-2.666) X^{3.54}$	0.908	82.60
Serrano	$Y = (-1.097) X^{2.63}$	0.858	73.69
Lumptail searobin	$Y = (-2.030) X^{3.44}$	0.944	89.25
Panama hake	$Y = (-2.091) X^{2.71}$	0.973	94.72
Pacific porgy	$Y = (-2.238) X^{3.9}$	0.948	89.88
Longfin sanddab	$Y = (-1.507) X^{3.6}$	0.979	95.90
Specklefin midshipman	$Y = (-3.756) X^{3.85}$	0.961	92.38
California lizardfish	$Y = (-2.65543\,E\text{-}3) X^{3.01}$	0.867	75.17
Yellowbelly lizardfish	$Y = (-0894) X^{3.69}$	0.854	73.09

*Intercept in parenthesis is equal to Log of a. $P = 0.01$ for all equations.

Table 4

Regression equations for fish weight (Y) vs. fish length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	Equation* $Y = a X^b$	Correlation coefficient	Percent r^2
Bigmouth sole	$Y = (-4.131) X^{3.03}$	0.978	95.68
Pink cusk eel	$Y = (-14.51) X^{3.46}$	0.968	93.86
Basketweave cusk eel	$Y = (-4.955) X^{3.05}$	0.964	93.04
Serrano	$Y = (-3.497) X^{2.82}$	0.976	95.34
Lumptail searobin	$Y = (-11.509) X^{3.15}$	0.988	97.74
Panama hake	$Y = (-11.213) X^{2.95}$	0.981	96.41
Pacific porgy	$Y = (-2.684) X^{2.75}$	0.984	97.01
Longfin sanddab	$Y = (-13.13) X^{3.46}$	0.992	98.59
Specklefin midshipman	$Y = (-5.001) X^{3.16}$	0.981	96.43
California lizardfish	$Y = (-4.953) X^{3.0}$	0.962	92.65
Yellowbelly lizardfish	$Y = (-5.801) X^{3.31}$	0.979	96.01

*Intercept in parenthesis is equal to Log of a. $P = 0.01$ for all equations.

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Responsiveness of Starved Northern Anchovy *Engraulis mordax* Larvae to Predatory Attacks by Adult Anchovy

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Most studies of larval mortality have been on food, feeding, and starvation, with less work done on predation and even fewer studies on the interaction between starvation and predation (Hunter 1984). Vulnerability to predation is a product of the probability of encounter between prey and predator, and prey susceptibility (Bailey and Houde 1989). Starvation could affect one or both of these components: starving larvae might be less able to avoid attacks by predators than fed ones (Rothschild et al. 1982). On the other hand, a decrease in conspicuousness of starved larvae might reduce their probability of encounter with predators (Gamble and Fuiman 1987). In addition, slow growth caused by an inadequate food supply could result in larvae remaining in the length-classes most vulnerable to predation and thereby increase larval losses (Shepherd and Cushing 1980).

In northern anchovy *Engraulis mordax* larvae, vulnerability to predation by fishes is size-specific, thus slower growth could result in greater losses (Webb 1981, Folkvord and Hunter 1986). The objective of this study was to evaluate the effect of starvation on avoidance performance of northern anchovy. We estimated the responsiveness and escape ability of 9 mm SL (standard length) anchovy to predatory attacks by adult anchovy as a function of days of starvation. We also developed histological starvation criteria which link the nutritional condition of larvae to their responsiveness to attacks by fish predators. This could allow an assessment of the interaction between predation by fishes and starvation in the sea, because the nutritional condition of sea-caught larvae could be assessed using histological criteria (O'Connell 1976 and 1980, Theilacker 1978 and 1986).

Materials and methods

Rearing and experimental design

About 4000 northern anchovy eggs produced by a captive brood stock (Leong 1971) were placed in a 100-liter black fiberglass tank maintained at 16.0–17.4°C (mean 16.2° C). Except for minor differences, larvae were reared following the procedure outlined by Hunter (1976). Larvae were reared until they reached 9 mm live standard length (about 20 days posthatch) at which time they were used in our experiments. In the experiments, 9 mm larvae were used because smaller anchovy larvae respond less frequently (<36%) to predators (Folkvord and Hunter 1986).

When larvae reached 9 mm, they were separated into two groups by transferring about half of them to another 100-liter tank containing only filtered seawater. The transferred larvae were never fed. Avoidance performance of the starved larvae was compared with that of larvae fed daily in the original tank. Initially a series of tests was conducted to estimate if the transfer of larvae affected avoidance performance. In these tests both groups were fed and one was transferred. Mortality was higher in the transferred group over the first day, but no significant difference existed between the groups thereafter in mortality or in their response to predators using the behavioral methods outlined below.

Larvae from three different rearing groups were used. In two groups, none of the starved larvae survived more than 6 days, and in one group a few survived 7 days. Considering all groups together, about 50% of the starved larvae survived 4–5 days and only 1% survived 7 days of starvation. Thus, most of the data are for larvae starved for 1–5 days. Four groups of five adult anchovy (90–107 mm SL) were used as predators. Predators were placed in the test container (a fiberglass tank 0.75 × 2.15 × 0.83 m with a glass window on one side) about 3 weeks prior to a series of experiments. Ambient seawater

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(15.1–17.8°C) flowed continuously through the tank, except during the experiments when water flow was stopped. Two household tungsten lamps above the tank provided about 2000–3000 lux at the water surface.

The experimental procedure was similar to Folkvord and Hunter (1986). Experiments were run in the morning and early in the afternoon starting about 24 hours after onset of starvation. Adult brine shrimp (*Artemia* sp.) were used to identify variation in predator feeding behavior between and during experiments. The addition of three brine shrimp or three starved anchovy larvae or three fed anchovy larvae constituted a single trial. Each experiment started with 3 *Artemia* trials followed by 15 trials repeating the sequence; fed larvae, starved larvae, and *Artemia*. The initial three brine shrimp trials insured that the feeding performance of the predators was stable, and subsequent brine shrimp trials were to check for effects of satiation (Folkvord and Hunter 1986). The brine shrimp trials were also used to test for differences in feeding performance among predator groups. No significant differences existed among the 4 predator groups in the proportion of brine shrimp eaten in 5 minutes (99% of the brine shrimp were eaten), or in the proportion of fed or starved larvae responding to attacks (logistic regressions, $P>0.40$).

A trial began when the prey were gently poured from a beaker into the test container and ended when all three prey were consumed or when 5 minutes had elapsed. During a trial, each time a prey was attacked by a predator, we recorded whether or not the prey responded to the attack, whether or not it escaped, and the time required to capture the prey. A predator attack was defined as a change in swimming speed or direction towards a prey followed by an opening of the mouth. A response to a predator was defined as a change in larval swimming speed or direction that occurred during an attack. An escape was defined as a predator attack in which the larva responded and successfully avoided the predator. A total of 345 fed and 345 starved larvae were used in the experiments, but the results are based on the number of predatory attacks and not on the total number of larvae tested. Some larvae were attacked more than once and others were not attacked at all. If a larva was attacked more than once in an experiment, each interaction was considered a separate event. When a larva was taken immediately after release or before it had moved, the interaction was not assessed. The responsiveness to attacks was assessed in 295 out of 325 attacks by predators on fed larvae and in 266 out of 323 attacks on starved larvae.

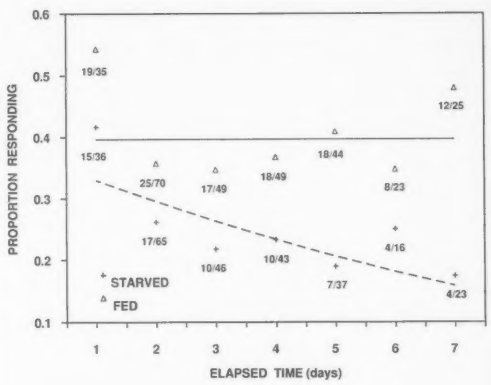

Figure 1

Proportion of fed and starved 9 mm SL northern anchovy larvae that responded to attacks of adult northern anchovy (Y), as a function of the duration of the starvation period (X = elapsed time in days). Horizontal line represents average proportion of fed larvae responding (0.4 ± 0.03); logistic regression, effect of day, $P>0.8$. Dashed line for starved larvae is given by the equation: $Y=e^{(-0.55-0.16*X)}/(1+e^{(-0.55-0.16*X)})$; logistic regression, effect of day, P 0.044. Numbers next to points are number of responses and interactions.

Assessment of nutritional condition

Histological criteria were developed to link starvation-induced changes in avoidance behavior of larvae to their nutritional condition. Samples of starved and fed larvae from each of the three groups were taken for histological analysis. Twenty starved and 10 fed larvae were collected every morning starting about 24 hours after onset of starvation. Larvae were fixed in Bouin's solution, embedded in Paraplast-plus, serially sectioned at 5 μm, and stained with Harris hematoxylin eosin-phloxin B.

O'Connell (1976) found that pancreas condition, notochord shrinkage and muscle fiber separation were the histological characteristics that best distinguished starving anchovy larvae from healthy ones during the first feeding stage (4 mm SL, about 4 days posthatch). These characteristics did not prove to be useful for the diagnosis of starvation in the 9 mm (20 day posthatch) larvae. For example, fibers of the trunk musculature were perfectly arrayed in starved 9 mm larvae, and no interfiber spaces existed in any of the larvae analyzed even after 6 days of starvation. We also found no correlation between the condition of the notochord and starvation. Also presence, size, and abundance of hindgut vacuoles were interpreted as indicators of recent feeding and not of larval condition.

The histological condition of the liver proved to be the best character for diagnosis of starvation in 9 mm larvae. Liver condition has been used for the diagnosis of starvation in fishes in combination with other characters by O'Connell (1976), Theilacker (1978), and Watanabe (1985), and liver alone was used by Storch and Juario (1983) and Storch et al. (1984). In the results section, we relate histological condition of the liver to days of starvation and responsiveness to predatory attacks.

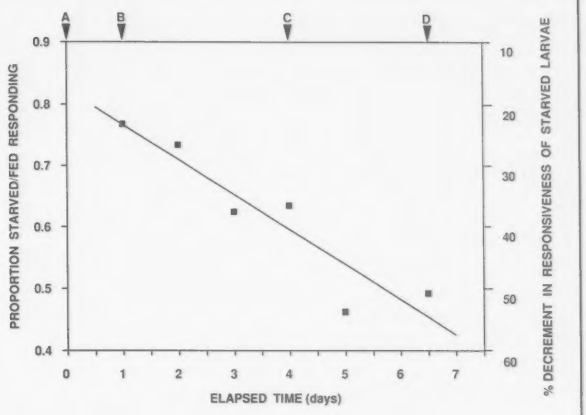

Figure 2

Responsiveness to anchovy predators of starved northern anchovy larvae (relative to fed larvae tested in the same experiment) shown in relation to duration of the starvation period and the condition of larval hepatic tissue. Data from days 6 and 7 were combined to obtain sufficiently high numbers of starved larvae. Equation for the line is $Y = 0.824 - 0.057X$ (R^2 0.87, SE est. 0.05). Histological characteristics of the liver of starved larvae are indicated with letters and arrows. (A) Glycogen vacuoles in hepatocytes, (B) no glycogen, structures unaltered, (C) hepatocytes membranes damaged, dark nuclei, and (D) cell atrophy, nuclei pycnotic and irregular.

Results

Response and escape probabilities

The proportion of larvae responding to attacks of adult anchovy progressively decreased with starvation. Forty percent of fed larvae responded to the attacks of predators, about the same proportion determined for 8.5 mm anchovy by Folkvord and Hunter (1986, test of binomial proportions, P 0.64). After 4 days of starvation 23% responded, and by 7 days of starvation 17% responded (Fig. 1). The higher value for both fed and starved larvae on day 1 could partly be due to the predator inexperience in preying on anchovy larvae, since during the acclimation period the predators had been fed only live adult *Artemia*.

Considerable variability existed in the percentage of larvae that responded to predators in the fed groups from day to day (range of daily averages 35–54%) and among predator and prey groups (range of group averages 36–45%). Since a series of trials using fed larvae always accompanied those with starved larvae, it was possible to adjust for this interexperiment variability by dividing the fraction of starved larvae that responded by the fraction of fed larvae that responded during the same experiment. After one day of starvation (that is, 24–30 hours after transfer) this ratio was 0.77, indicating that the response probability for larvae deprived of food for 1 day was 23% lower than that of fed larvae. The regression for these calculated ratios indicates that larvae starved for 4 days were 40% less likely to respond than fed larvae, and those starved for 7 days were 58% less likely to respond (Fig. 2).

Very few larvae escaped predators regardless of their nutritional state. Thus, it was not possible to evaluate the proportions escaping as a function of the duration of starvation. Considering all data combined, starved larvae were less successful in escaping predators (0.8% vs. 3.4% fed larvae; test of binomial proportions, P 0.027). Escape probabilities were lower in fed larvae in this study (3.4%) than in Folkvord and Hunter (1986, 12%) for 8.5 mm larvae (test of binomial proportions, P 0.01). Some obvious differences existed between the studies. In the present study, body size of the anchovy predators was about 10% longer, temperature in the experimental tank about 5°C lower, and the test tank acclimation period of predator groups was longer. Any of these factors could affect the probability of escape.

Relation between prey responsiveness and histological condition

Larvae deprived of food for 1 day had no vacuoles in their liver, but cellular structures showed no alterations (Fig. 3). The vacuoles seen in fed larvae presumably contain glycogen (O'Connell and Paloma 1981). Disappearance of vacuoles after 24 hours of food deprivation has also been observed by Watanabe (1985) in freshwater gobiid larvae reared at 15–20°C. At this stage of starvation, anchovy larvae were 23% less responsive to predators than were fed larvae. After 4 days of starvation, the hepatic tissue began to deteriorate; cell outlines were hardly distinguishable, and the nuclei stained darkly. Larvae with these characteristics were about 40% less responsive than were fed larvae.

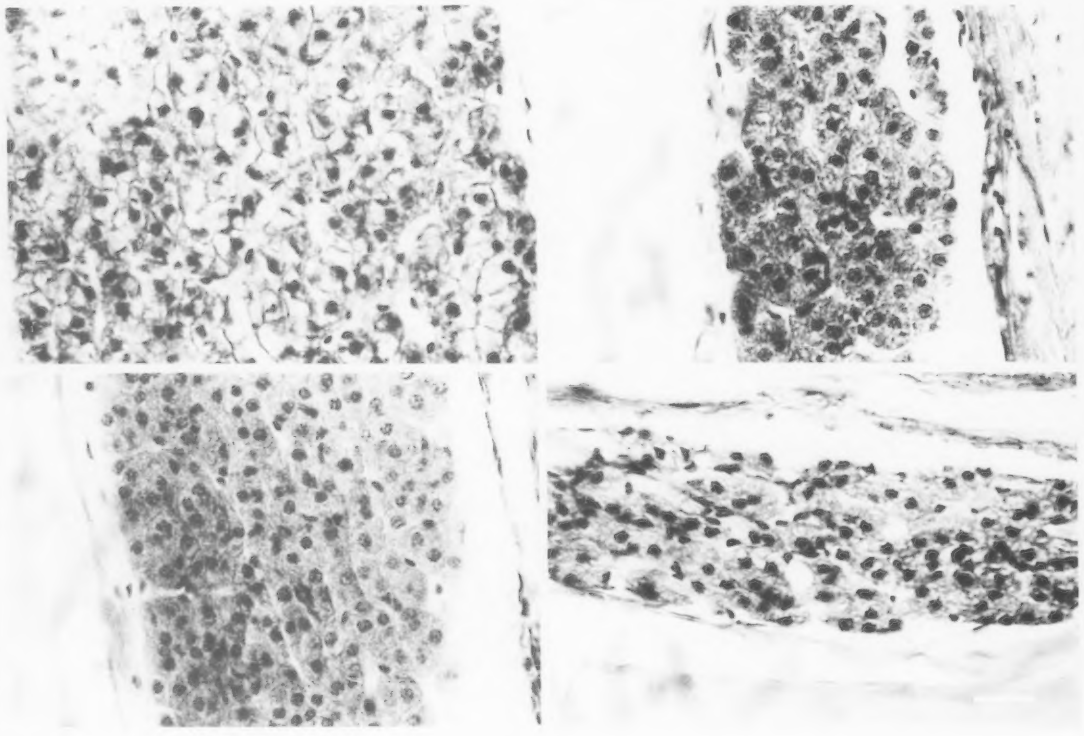

Figure 3

Condition of the hepatic tissue of larval northern anchovy after 0, 1, 4, and 6 days of starvation (white bar = 0.01 mm). (Upper left) fed larvae. White vacuolated areas may be glycogen deposits. (Upper right) 1 day of starvation. No vacuolated areas and no cellular deterioration. (Lower left) 4 days of starvation. Damaged membranes and dark nuclei. (Lower right) 6 days starvation. Hepatocytes atrophied, nuclei shrunken and pycnotic.

Hepatocytes of larvae starved for 6–7 days had atrophied, making the nuclei appear to be more densely distributed. Nuclei were pycnotic and irregular in shape. Such larvae were about 55% less responsive to predators than fed larvae.

Discussion

Starvation may affect responsiveness of larger anchovy larvae in a fashion similar to the one here described for 9 mm larvae. Preliminary measurements by Folkvord (1985) indicated that newly metamorphosed juvenile anchovy (35 mm SL) were less likely to respond if deprived of food. When deprived of food for 5 days, only 50% of the fish responded to predatory attack whereas 100% of fed fish did so. Håkanson (1989) analyzed the lipid contents of fed and starved anchovy larvae of similar age and reared at similar temperatures as in this study. He found a decrease in the content of triacylglycerol, an energy storage component, after 3 days of starvation. On the other hand, we found that the glycogen reserve in the liver was nearly depleted after one day of starvation. Lipid reserves greatly increase after metamorphosis (J.R. Hunter, unpubl. data) and consequently such a decrement in avoidance behavior with a few days of food deprivation may be limited to the larval and early juvenile period. Yin and Blaxter (1987) also determined a decrease in the response rates of unfed yolksac herring, cod and flounder larvae to tactile stimuli, especially after the point of no return (PNR). These authors determined a similar effect in the response rate of older Clyde herring larvae (36 days, 14 mm) to contact with a pipette after the PNR (6 days of starvation at 9–10 °C). A starvation-induced decrease in vulnerability to

predation because of a decrease in encounter rates between predators and prey (Gamble and Fuiman 1987) is not supported by our data. A decrease in encounter rates does not seem to have occurred, since attack rates on fed and starved larvae were the same. A change in larval activity may, however, have a greater effect on prey visibility among smaller larvae than larger ones.

Our scale of nutritional condition based on liver characteristics could be used to assess the extent of the interaction between starvation and predation in the sea. The level of cell deterioration found in larvae starved 4 days or more at 16°C most likely represents the PNR, and the starvation-induced vulnerability to predation could amplify the losses caused by starvation only up to this point. A sharp decline in cholesterol and polar lipid content was found in larval anchovy after 5 days of starvation at 15.5°C (Håkanson 1989). These lipids are cell membrane constituents. The high vulnerability of larvae starved for periods longer than 4–5 days seems of less ecological consequence, since nearly all such severely emaciated larvae would probably ultimately die of starvation. However, the increase in vulnerability over the entire starvation period is of interest, because it may affect estimates of starvation rates in the sea and possibly estimates of natural larval mortality. Clearly, rates of starvation based on daily incidence of starvation classes (Theilacker 1986) may underestimate the actual losses if starvation results in an increase in the vulnerability to predators. In addition, our results may support the hypothesis of Isaacs (1964) that daytime plankton samplers may be selective for weaker and less-responsive larvae. Such a hypothesis requires vision to be the primary sensory modality for the larval avoidance response. If this were the case, the reduced responsiveness caused by starvation could result in daytime plankton catches containing proportionately more starving larvae than those taken at night.

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Sea Turtle Strandings and Shrimp Fishing Effort in the Northwestern Gulf of Mexico, 1986-89

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Incidental capture of sea turtles in shrimp trawls is the most important human cause of sea turtle mortality (Magnuson et al. 1990). Offshore stocks of penaeid shrimp were discovered in the Gulf of Mexico in the mid-1930s, and expansion of the offshore shrimp fishery began in the late 1940s following World War II (Whitaker 1973, Krauthamer et al. 1984, Tetty and Griffin 1984, Rayburn 1989). The industry continued to expand and improve its fishing technology into the 1980s. During the same period when shrimping effort was increasing and harvesting technology was improving, the abundance of sea turtles declined (Magnuson et al. 1990).

Sea turtle strandings along coastal shorelines of the southeastern United States have been used as one index of mortality due to shrimping (Magnuson et al. 1990). An increase in sea turtle strandings during commercial penaeid shrimp fishing seasons and a decrease with the closing of these seasons have been observed on the Atlantic coast of the southeastern United States (Hillestad et al. 1978, Talbert et al. 1980, Ruckdeschel and Zug 1982, Booker and Ehrhart 1989, Schroeder and Maley 1989). The relationship between sea turtle strandings and shrimp fishing in the northwestern Gulf of Mexico has received less attention (Rabalais and Rabalais 1980, Amos 1989, Whistler 1989, Magnuson et al. 1990), although Texas and Louisiana together produce most (almost 74% during 1986–89) of the offshore (seaward of barrier islands) commercial catch of penaeid shrimp in the southeastern United States. In this study, we used product-moment correlation analysis to test the null hypothesis that there was no relationship between monthly sea turtle strandings and shrimp fishing effort in the northwestern Gulf of Mexico coast during 1986–89.

Sea turtles would not be captured in shrimp trawls if the temporal-spatial distributions of sea turtles and shrimp fishing effort did not overlap to some extent. However, we have no a priori reason to expect that temporal-spatial distributions of sea turtles and shrimp fishing effort match exactly. Shrimp trawling in the northwestern Gulf varies seasonally and spatially as related to the annual cycle of occurrence and abundance of short-lived penaeid shrimp (Kutkuhn 1962, Neal and Maris 1985). It is most intense during spring and summer when surface waters are warm. Shrimp spawn in the Gulf where the eggs hatch and larvae develop as they are carried toward the estuaries in spring and early summer. As postlarvae, shrimp enter the estuarine nursery areas where they grow for several months before emigrating to the Gulf and becoming vulnerable to the offshore shrimp fishery. There they continue to grow and migrate to deeper waters to spawn while being exploited by the fishery. In contrast, sea turtles are long-lived and can be exposed to mortality risks for decades. Based on strandings, commercial and recreational fishing bycatch, and aerial surveys, sea turtles are most abundant in the northwestern Gulf during spring or early summer, with a lesser peak in abundance in autumn (Hildebrand 1982, Fritts et al. 1983, Thompson 1988, Magnuson et al. 1990). Waters of the northwestern Gulf are foraging habitat for the turtles, and they are used as migratory routes when the turtles move northward in spring and southward in autumn (Hildebrand 1982, 1983). The most numerous species in the

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northwestern Gulf are the loggerhead *Caretta caretta* and Kemp's Ridley *Lepidochelys kempi* (Rabalais and Rabalais 1980, Thompson 1988, Amos 1989, Whistler 1989).

This study deals with monthly sea turtle strandings along shorelines and shrimp fishing effort seaward of shorelines in the northwestern Gulf. Strandings are observed for the most part on barrier beaches, so they can be summarized in linear distance units of shoreline. Shrimp fishing effort is reported as days fished within spatial units represented by shrimp statistical subareas and 5-fathom (fm, 9.1 m) depth intervals (Kutkuhn 1962, Patella 1975). To test the null hypothesis, we paired monthly strandings along segments of shoreline with monthly shrimping effort within 5-fm depth intervals in the adjacent offshore waters. This was done because it was expected that the farther offshore the shrimping took place, the less likely sea turtles impacted by such shrimping would reach the shoreline, due to combined effects of surface currents, winds, waves, tides, action by scavengers (e.g., sharks) and decomposition of turtle carcasses (Heinly et al. 1988, Murphy and Hopkins-Murphy 1989, Shoop and Ruckdeschel 1989, Whistler 1989). Also, it is possible that temporal-spatial distributions of sea turtles and shrimp fishing activities overlap only within certain depth intervals (Magnuson et al. 1990).

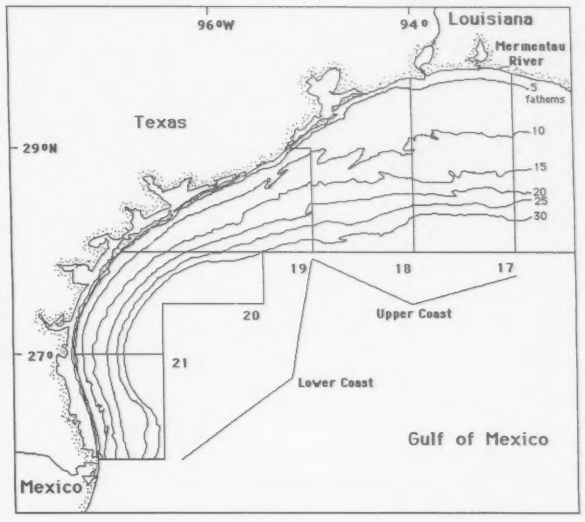

Figure 1
Boundaries of upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) and 5 fm (9.1 m) depth intervals of the northwestern Gulf of Mexico (see Kutkuhn 1962, Patella 1975).

Materials and methods

Since 1980, sea turtle strandings along the coasts of the southeastern United States have been compiled by the Sea Turtle Stranding and Salvage Network (STSSN, Schroeder 1989). Shrimp fishing effort statistics in the Gulf have been compiled since 1956 (Kutkuhn 1962). Our analyses were based on data from 1986–89, including sea turtle strandings available from the STSSN database at the National Marine Fisheries Service's (NMFS) laboratory in Miami, Florida, and shrimp-fishing effort data available from the NMFS laboratory in Galveston, Texas.

Schroeder (1989) described the STSSN and procedures used to document sea turtle strandings. State coordinators review and verify the stranding data submitted by network participants, then forward them to the NMFS laboratory in Miami, Florida, where the database is maintained. The database is not independent of the distribution of human-induced mortality factors, temporal-spatial coverage is rarely uniform, and most beaches are surveyed by volunteers (Magnuson et al. 1990). To improve temporal-spatial coverage and supplement voluntary coverage, the NMFS Galveston Laboratory initiated year-round surveys along the coasts of southwestern Louisiana and Texas in 1986 (Heinly et al. 1988). Four-wheel-drive trucks, off-road motor cycles, or all-terrain vehicles were used to survey accessible gulfside shorelines at least once per month, from the Mermentau River, Louisiana, to the Texas–Mexico border (Fig. 1). The National Park Service surveyed the Padre Island National Seashore near Port Aransas, Texas, and the U.S. Fish and Wildlife Service and Texas Parks and Wildlife Department assisted in surveying Matagorda I. near Port O'Connor, Texas. Reconnaissance flights conducted at least once monthly were used to search for stranded turtles on San Jose I. near Corpus Christi, Texas.

For our analyses, sea turtle strandings (all species combined) in the northwestern Gulf of Mexico during 1986–89 were extracted from the STSSN database. Records of turtles caught by various commercial and recreational fishing methods were deleted. Also deleted were strandings of head-started (captive-reared) sea turtles, because their distribution is influenced to some extent by where they are released (Manzella et al. 1988, Fontaine et al. 1989).

The monthly sea turtle strandings and shrimp fishing effort were separated into two geographic zones: the upper coast (subareas 17–18) and lower coast (subareas 19–21). This was done because the upper coast has a wider continental shelf than the lower, so the distance a dead, sick, or injured sea turtle would have to travel from a particular depth interval to the shore is greater on the upper coast than on the lower (Fig. 1). Due to difficulty of access, the small portion of subarea 17 east of the Mermentau River in southwestern Louisiana was not surveyed for strandings, so approximately 86% of the coastline of the upper coast zone was surveyed for turtle strandings (Table 1). For this reason, we included in the upper coast zone only those turtle strandings that occurred west of the Mermentau River. We could not place a similar boundary restriction on the fishing effort data, so the eastern boundary of subarea 17 marked the eastern boundary of the upper coast in this regard. However, strandings and fishing effort were standardized to strandings per linear distance of shoreline and to days fished per unit area, respectively, so the exclusion of strandings east of the Mermentau River should have had little if any effect on our results.

Our analyses included fishing effort from the six 5-fm intervals between 0 and 30 fm (54.9 m) in shrimp statistical subareas 17–21. We did not include effort data beyond 30 fm, because only 6% of the shrimping effort on the upper coast and 8% on the lower coast occurred seaward of 30 fm during 1986–89 (Table 2).

Table 1

Extent of accessible shoreline surveyed for sea turtle strandings during 1986–89 compared with total shoreline within the upper and lower coasts of northwestern Gulf of Mexico[1].

Zone	Shrimp statistical subarea[2]	Shoreline: Accessible (km)	Shoreline: Total (km)	Shoreline: Percent of total
Upper coast	[3]17–18	212	245	86.5
Lower coast	19–21	408	420	97.1
Total	[3]17–21	620	665	93.2

[1]Derived from measurements made using dividers on National Ocean Service (NOAA) nautical charts.
[2]Figure 1; see also Kutkuhn (1962).
[3]Only the accessible shoreline west of the Mermentau River, Louisiana, was surveyed for strandings in subarea 17.

Table 2

Distribution of shrimp fishing effort on the upper and lower coasts of northwestern Gulf of Mexico by depth, 1986–89.[1]

Depth: fm	Depth: m	Percent of shrimp fishing effort: Upper coast[2]	Percent of shrimp fishing effort: Lower coast[3]
0–5	0.0–9.1	28	5
5–10	9.1–18.3	27	13
10–15	18.3–27.4	16	20
15–20	27.4–36.6	10	26
20–25	36.6–45.7	7	18
25–30	45.7–54.9	6	10
30–50	54.9–91.4	6	8
Total		100	100

[1]Adapted from data provided by Frank Patella, NMFS Galveston Lab., pers. commun., June 1990.
[2]Shrimp statistical subareas 17 and 18 (Fig. 1; see also Kutkuhn 1962).
[3]Shrimp statistical subareas 19–21 (Fig. 1; see also Kutkuhn 1962).

Monthly sea turtle strandings within the upper and lower coasts were standardized by dividing them by distance of accessible shoreline (Table 1) in these two zones, respectively, to obtain the monthly turtle strandings per 100 km (S). We used the amount of surface area within shrimp statistical subareas and 5 fm depth intervals, as determined by Patella (1975), to standardize monthly fishing effort within the upper and lower coasts by depth interval. The surface area within a depth interval was usually greatest nearshore and decreased seaward in both zones (Fig. 1). For each 5-fm depth interval, monthly fishing effort in the upper and lower coast zones was divided by the surface area of the geographic unit (zone × depth interval) within which the effort occurred, to standardize effort to a measure of shrimping intensity. Standardized fishing effort per unit area (E) was expressed as days fished per 100 km^2.

Product-moment correlation analysis requires that the two variables have normal distributions. Neither standardized strandings (S) nor fishing effort (E) were normally distributed, as shown by large departures of their skewness and kurtosis coefficients from zero (Table 3). Therefore, we logarithmically transformed both variables, after adding 1 to each value of S and E (because some values were zero). The logarithmically transformed variables had skewness and kurtosis coefficients closer to zero, thus approaching normality. For each of the 12 combinations of two geographic zones and six depth intervals, product-moment correla-

Table 3
Descriptive statistics for untransformed and transformed monthly sea turtle strandings and shrimp fishing effort for the upper and lower coasts of northwestern Gulf of Mexico during 1986–89.

	Sea turtle strandings[1]		Shrimp fishing effort[2]	
	Upper coast	Lower coast	Upper coast	Lower coast
Untransformed				
n	48	48	288	288
Mean	4.16	3.18	13.26	17.82
Variance	43.15	9.15	509.35	374.03
Skewness coeff.	2.66	1.98	4.32	4.46
Kurtosis coeff.	7.60	4.50	22.37	31.84
Minimum	0.0	0.0	0.0	0.0
Maximum	31.7	14.7	170.1	197.4
Transformed[3]				
n	48	48	288	288
Mean	1.13	1.23	2.07	2.57
Variance	0.92	0.38	1.01	0.80
Skewness coeff.	0.66	0.36	0.51	−0.41
Kurtosis coeff.	−0.29	−0.05	0.23	0.44
Minimum	0.0	0.0	0.0	0.0
Maximum	3.49	2.75	5.14	5.29

[1]Per 100 km of accessible shoreline.
[2]Per 100 km^2 of surface area.
[3]To natural logarithms after addition of 1 to each observation.

tions between 48 pairs (12 months × 4 years) of ln (S + 1) and ln(E + 1) were determined.

Results

Scatter plots for geographic zones and depth intervals for which ln(S + 1) was significantly ($P<0.05$) correlated with ln(E + 1) are shown in Figure 2. On the upper coast, the three correlation coefficients, r, that differed significantly from zero were positive and occurred with fishing effort in the 0–5, 5–10, and 10–15 fm intervals. On the lower coast, r was significantly different from zero and positive only with fishing effort in the 5–10 and 10–15 fm intervals. These correlations indicated that turtle strandings increased as fishing effort increased in waters landward of 15 fm. Correlation coefficients for fishing effort in other depth intervals within the two zones did not differ significantly from zero.

The five significant correlations ($P<0.05$) were detected despite the relatively coarse temporal-spatial scale of the data sets (Fig. 2). Although they were of moderate strength, ranging from 0.327 to 0.512, even the lowest among them had a very small probability (P 0.0232) of occurring due to chance alone (Fig. 2). P was even smaller for the other four significant correlations. There was no significant ($P>0.05$) heterogeneity among the five correlation coefficients.

The means of the transformed strandings for the upper and lower coasts did not differ significantly (Table 3). However, the upper coast exhibited more months in which there were no strandings than did the lower coast (Fig. 2). The mean of transformed fishing effort on the lower coast was significantly higher than that for the upper coast, indicating a higher average fishing intensity on the lower than upper coast in waters landward of 30 fm.

Loggerheads and Kemp's Ridleys occurred most frequently in the strandings, followed by hawksbills *Eretmochelys imbricata*, greens *Chelonia mydas*, and leatherbacks *Dermochelys coriacea* (Table 4). Turtle strandings occurred year-round with peaks in April and May, and with a secondary peak in August. Annual strandings declined over the years covered by the study, with 417, 259, 188, and 183 strandings reported in 1986–89, respectively.

Discussion

The distributions of sea turtles and shrimp trawling must overlap to some degree because it is well documented that sea turtles are caught in shrimp trawls

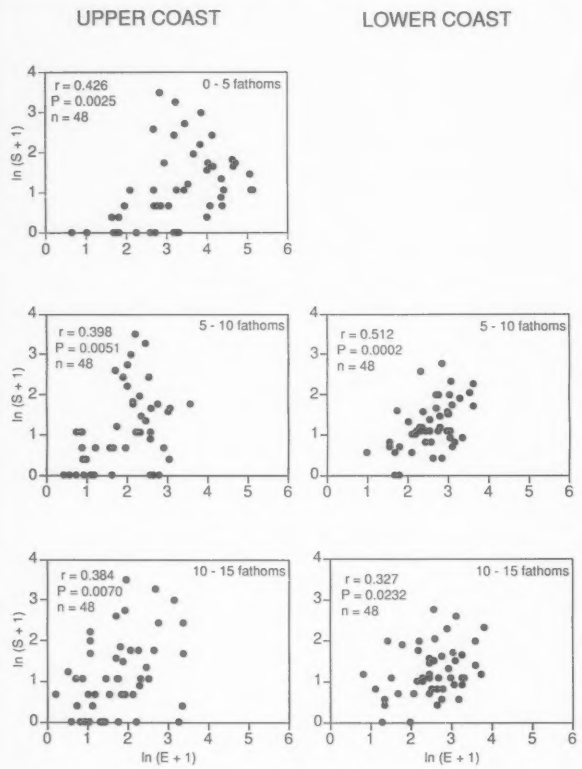

Figure 2

Scatter plots for significant ($P<0.05$) correlations between transformed monthly sea turtle strandings, ln(S + 1), and transformed monthly shrimp fishing effort, ln(E + 1), on upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) of the northwestern Gulf of Mexico during 1986–89.

(Murphy and Hopkins-Murphy 1989, Magnuson et al. 1990). In fact, sea turtles may congregate in shrimping areas to feed on discarded bycatch (Shoop and Ruckdeschel 1982, Ruckdeschel and Shoop 1988). However, no cause-and-effect relationship between sea turtle strandings and shrimping has been demonstrated to date.

It is noteworthy that our analyses detected significant correlations despite the wide variation inherent in turtle stranding and fishing effort data. These significant positive correlations are circumstantial evidence of a linkage between strandings and shrimping, but do not demonstrate that the strandings were caused by shrimping. Strandings and shrimping occur year-round and both are strongly seasonal, with peaks during warm months. The correlations we detected are consistent with earlier findings that incidental capture in shrimp trawls is the major cause of sea turtle mortality associated with human activities, but it is also recognized that other fisheries, dredging, collisions with boats, oil-rig removal with underwater explosives, entrainment in power plants, and directed take contribute to sea turtle mortality at sea (Magnuson et al. 1990).

Interpretation of statistical relationships between sea turtle strandings and shrimp trawling activity is confounded by the dynamics of waterborne transport of stressed, injured, or dead turtles to stranding sites. Surface currents, winds, waves, tides, and scavengers, as well as conditions affecting the buoyancy of turtles, can affect their transport toward or away from shore (Murphy and

Table 4

Species composition of sea turtle strandings in the northwestern Gulf of Mexico by month, summed over years 1986–89.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Loggerhead *Caretta caretta*	9	10	46	146	95	33	40	37	31	29	19	20	515
Kemp's Ridley *Lepidochelys kempi*	0	6	36	82	48	36	27	51	23	22	17	9	357
Hawksbill *Eretmochelys imbricata*	0	1	2	0	1	5	4	15	18	14	2	5	67
Green *Chelonia mydas*	1	0	5	7	6	6	2	2	0	4	1	4	38
Leatherback *Dermochelys coriacea*	0	0	1	8	5	3	0	1	0	2	3	0	23
Undetermined	0	0	6	6	2	5	10	4	5	6	1	2	47
Total	10	17	96	249	157	88	83	115	77	78	43	40	1047

Hopkins-Murphy 1989, Shoop and Ruckdeschel 1989, Whistler 1989). In the northwestern Gulf, tidal currents move water toward shore, and waves and surface drift transport floating objects to the beach from longshore currents (Collard 1990, Collard and Ogren 1990). Swimming and diving abilities may be reduced in stressed or injured sea turtles, causing them to remain at or near the surface while being transported more or less passively. The longer a carcass remains in the water, the longer it would be subjected both to decomposition and scavengers which could cause it to disarticulate, release bloating gases, and sink. Not all turtles that become stranded are documented by the STSSN. Thus, reported strandings of sea turtles provide an incomplete measure of those that are killed or injured by humans or that succumb to natural mortality factors at sea (Murphy and Hopkins-Murphy 1989).

On the upper coast, significant correlations were observed in 0–15 fm where 71% of the shrimp fishing effort on the upper coast occurred during 1986–89 (Table 2, Fig. 2). Significant correlations were observed on the lower coast in 5–15 fm where 33% of the lower coast effort occurred. Such correlations suggest that the impact of shrimping on sea turtles may occur within 15 fm seaward of the coastline, and this is consistent with the conclusion by Magnuson et al. (1990) that incidental capture of sea turtles in shrimp trawls occurs for the most part in depths up to 27 m (15 fm). However, on the lower coast 5% of the shrimp fishing effort occurred in the 0–5 fm interval, and we observed no significant correlation for that interval.

It is neither practical nor cost-effective to attempt characterization of all conditions and factors that influence whether sea turtles become stranded and where and when they become stranded in relation to various causes of mortality, injury, stress, or illness at sea. However, year-round coverage is essential to monitoring temporal variations, and it provides biological samples, specimens for necropsy, and other information that can be compared with human activities and oceanographic variables in examining the causes of strandings.

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Trophic Relationship of Age-0 and Age-1 Walleye Pollock *Theragra chalcogramma* Collected Together in the Eastern Bering Sea*

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Walleye pollock *Theragra chalcogramma* a gadid endemic to the north Pacific, is one of the most important components of the Bering Sea food web (Smith 1981) and supports the largest single-species commercial fishery in the world (Megrey 1989). Although a number of studies have documented the food habits of larval (e.g., Kamba 1977, Cooney et al. 1980, Clarke 1978 and 1984, Kendall et al. 1987, Grover 1990), juvenile (e.g., Kamba 1977, Bailey and Dunn 1979, Cooney et al. 1980, Lee 1985, Grover 1990), and adult walleye pollock (e.g., Takahashi and Yamaguchi 1971, Bailey and Dunn 1979, Livingston et al. 1986, Dwyer et al. 1987, Bailey 1989), previous studies have generally pooled samples either over time or space. While pooled data adequately characterize large-scale patterns of prey utilization, small-scale patterns of between-year-class trophic relationships are best defined by fish that were collected together.

This study examined the trophic relationship of age-0 and age-1 pollock that were collected in a single haul in the southeastern Bering Sea. As pollock are known to be highly cannibalistic (Takahashi and Yamaguchi 1971, Bailey and Dunn 1979, Livingston et al. 1986, Dwyer et al. 1987, Bailey 1989), this study looked for evidence of cannibalism, as well as defined the size and taxa of prey that were ingested by the two year-classes.

Methods

Juvenile pollock were collected as one aspect of a survey of groundfish in the eastern Bering Sea in 1985 by the *Morning Star*, using a Marinovich midwater trawl (Walters et al. 1988). An examination of length-frequency distributions from these trawls, which principally targeted age-0 fish, revealed that age-0 (zeros) and age-1 fish (ones) were rarely collected together (Jim Traynor, NMFS Alaska Fish. Sci. Cent., Seattle, unpubl. data). Among stations where zeros and ones occurred in the same haul, comparable numbers of both year-classes were obtained at only one station. Coincidentally, although not all of the ones were saved, this was the only station where both ones and zeros were preserved. This collection was made from 0900 to 0920 hours on 3 August 1985, at station 95 (56° 11.17′N, 162°18.36′W), in the southeast shelf region. Gear depth averaged 20 m, and water temperature was 6.5°C. The fish were frozen at sea. In the laboratory, they were defrosted in 10% formalin to facilitate the simultaneous separation and fixation of the specimens. All the preserved specimens from this collection were analyzed.

This study examined the diet of 52 age-0 and 22 age-1 fish. Age groups were determined based on length, using the categories of Dwyer et al. (1987)—age 0, 1–130 mm; age 1, 131–220 mm, which were based on Smith's (1981) Bering Sea data. For each fish, total length was recorded and the stomach was removed. Stomach contents were dissected out and identified. Due to prey condition, only copepods could be consistently identified to species. Extremely well-digested copepods were identified largely by their size and shape. No distinction was made between copepodite and adult stages. Copepods eggs, *Calanus marshallae*, *Pseudocalanus* sp., *Centropages abdominalis*, *Metridia* sp., *Acartia* sp., and *Tortanus discaudatus* were identified. *Calanus marshallae* and *Metridia* sp. were >2 mm in length. All other copepod species were <2 mm. Other prey were identified as amphipods, euphausiid furcilia/juveniles, mysids, decapod larvae, and fish scales. Well-digested euphausiids were enumerated based on eye counts.

Food particle-size selection was examined by measuring widths of all prey items that were not severely digested or broken. Widths were recorded from a total of 7291 prey items.

Diet was analyzed in terms of numerical percent composition (%N), volumetric percent composition (%VOL), frequency of occurrence (%FO), and the index of relative importance (IRI=[%N+%VOL]×%FO) (Pinkas et al. 1971). Volumes were calculated from prey dimensions for zeros (Grover and Olla 1987), and were measured directly for ones.

Results

Little overlap was seen in the size of prey that were ingested by age-0 pollock, which ranged from 26 to 64 mm TL ($\bar{x}$ 49.4 mm, SD 9.6), and

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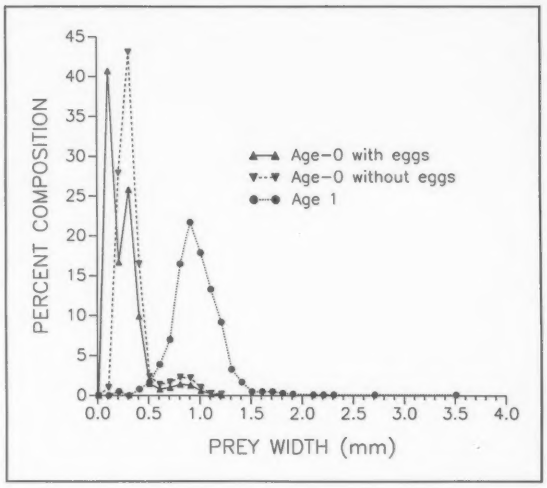
Figure 1

Size of prey ingested by age-0 and age-1 walleye pollock at station 95 (56°11.17′N, 162°18.36′W), in the southeastern shelf region of the Bering Sea, 3 August 1985. Age-0 data are plotted, including and excluding copepod eggs. Prey widths (in mm) were as follows: copepod eggs 0.11–0.20, *Calanus marshallae* 0.61–1.70, *Pseudocalanus* sp. 0.11–0.70, *Centropages abdominalis* 0.31–0.60, *Metridia* sp. 0.51–0.60, *Acartia* sp. 0.21–0.40, *Tortanus discaudatus* 0.31–0.50, amphipods 0.21–1.8, euphausiid furcilia/juveniles 0.21–3.50, mysids 0.41–0.50, decapod larvae 0.21–0.90. Fish scales were not included in this analysis, as their ingestion was deemed incidental.



by age-1 pollock, which ranged from 137 to 212 mm TL ($\bar{x}$ 162.8 mm, SD 16.32) (Fig. 1). Prey-size distributions were significantly different regardless of whether copepod eggs were included ($P<0.001$, Kolmogorov-Smirnov test; Conover 1980). Taxa of prey ingested by the two age-classes also differed (Table 1). Small copepods (0.21–0.50 mm width) and copepod eggs (0.11–0.20 mm width) comprised the bulk of the prey ingested by age-0 fish, while larger copepods and euphausiid furcilia (0.71–1.30 mm width) comprised the bulk of the prey ingested by age-1 fish.

Although euphausiid furcilia and juveniles made a substantial contribution to the diet of both age-classes, age-0 fish ingested smaller and/or earlier furcilia stages than did age-1 fish. Copepods comprised a major por-

Table 1

Composition of the diet of age-0 and age-1 walleye pollock *Theragra chalcogramma* in terms of index of relative importance (%IRI) and its components (%N, %VOL, and %FO). Values in parentheses exclude copepod eggs.

	Age-0				Age-1			
	%N	%VOL	%FO	%IRI	%N	%VOL	%FO	%IRI
Copepods								
Eggs	32.8	0.4	92.3	18.4				
Calanus marshallae	0.1 (0.2)	2.2 (2.2)	9.6	0.1 (0.1)	63.1	48.8	100.0	56.6
Pseudocalanus sp.	61.3 (91.3)	47.6 (47.8)	98.1	64.2 (81.8)	0.2	<0.1	13.6	<0.1
Centropages abdominalis	<0.1 (<0.1)	<0.1 (0.1)	3.8	<0.1 (<0.1)				
Metridia sp.	<0.1 (<0.1)	0.1 (0.1)	1.9	<0.1 (<0.1)				
Acartia sp.	0.1 (0.1)	<0.1 (<0.1)	5.8	<0.1 (<0.1)				
Tortanus discaudatus	<0.1 (<0.1)	<0.1 (0.01)	3.8	<0.1 (<0.1)				
Amphipods	<0.1 (<0.1)	<0.1 (<0.1)	3.8	<0.1 (<0.1	1.1	2.6	63.6	1.2
Euphausiid furcilia/juveniles	5.5 (8.2)	49.5 (49.7)	51.9	17.2 (18.0)	35.0	48.1	100.0	42.0
Mysids					<0.1	<0.1	4.5	<0.1
Decapod larvae					0.4	0.4	31.8	0.1
Fish scales					0.2	<0.1	27.3	<0.1

tion of the diet for both age groups, however age-0 fish primarily ingested small (<2mm in length) *Pseudocalanus* sp., while age-1 fish primarily ingested larger (>3mm) *Calanus marshallae* (Table 1).

Fish scales were observed in the stomachs of six age-1 fish. Only one scale was found in each stomach, and no other evidence of piscivory was observed. The scales were most likely ingested incidentally as a result of the collection process.

The mean number of prey ingested by age-0 fish was 134.8 (90.6 excluding copepod eggs), while age-1 fish ingested an average of 156.3 prey items. The incidence of feeding was 100% for both age groups.

Discussion

Based on two age and growth relationships (Nishimura and Yamada 1984, Yoklavich and Bailey 1989) and the timing of spawning in the southeast shelf region of the Bering Sea in 1985 (Mulligan et al. 1989), the age of age-0 pollock in this study was estimated to be 2–4 months. Assuming that the age-1 fish in this study were spawned as well as collected in the southeast shelf region, and then based on when spawning occurred in this region in 1984 (Hinckley 1987), the age of age-1 pollock was estimated to be 13–16 months.

At the time and place of this collection, diets of the two year-classes were divergent in terms of both prey size and taxa. Older, larger fish ingested larger prey. The importance of small copepods, notably *Pseudocalanus* sp., in the diet of age-0 pollock is consistent with previous studies (Kamba 1977, Cooney et al. 1980, Lee 1985, Grover 1990); however, one suborder of copepods, Cyclopoida, that was included in earlier dietary accounts was noticeably absent in the present study. Although, by most accounts, cyclopoids were not primary prey, Lee (1985) reported that for pollock between 20.0 and 24.9mm TL and 45.0 and 49.9mm TL, these copepods were either the foremost or second-most important prey in the southeastern Bering Sea. Differences between studies may reflect temporal or spatial patchiness of prey.

Large numbers of copepod eggs have previously been reported in the diet of juvenile pollock (Cooney et al. 1980, Lee 1985, Grover 1990). The eggs were probably ingested incidentally, as the dominant copepod in the diet of age-0 pollock, *Pseudocalanus* sp., carries its eggs (Corkett and McLaren 1978).

The diet of age-1 pollock was dominated by a large copepod, *C. marshallae*, and euphausiid furcilia and juveniles. While previous dietary accounts have also illustrated the importance of large copepods, other specifics of diet apparently vary seasonally and spatially. Bailey and Dunn (1979) found that in the eastern Bering Sea, amphipods replaced euphausiids in the diet of pollock <24cm in the summer of 1974. Dwyer et al. (1987) reported that copepods were the only prey ingested by pollock <30cm in the southeastern Bering Sea during the summer, although in the northwestern Bering Sea euphausiids and larvaceans were also a part of the summer diet. The absence of copepod eggs from the diet of age-1 fish is consistent with the fact that *C. marshallae* females broadcast rather than carry eggs (Peterson 1980).

Another trophic relationship reported for these two year-classes is cannibalism (Livingston et al. 1986, Dwyer et al. 1987). While adult pollock cannibalize age-0 pollock to some extent during all seasons in the eastern and southeastern Bering Sea, age-1 pollock (<30cm) have been observed to be cannibalistic only during autumn (Livingston et al. 1986, Dwyer et al. 1987). In the present study, based on a collection in summer, no conclusive evidence of piscivory or cannibalism was observed. Cannibalism has been shown to be highest when the vertical distribution patterns of juveniles and adults overlap (Bailey 1989). As this collection was not vertically discrete, the extent to which vertical distributions of age-0 and age-1 pollock overlapped at station 95 is unclear. However, based on the short duration and nature of this collection, i.e., that it targeted a hydroacoustic trace at a specific depth (Jim Traynor, NMFS Alaska Fish. Sci. Cent., Seattle, pers. commun. May 1991), then, minimally, vertical juxtaposition of the two year-classes is suggested. In which case, the present data indicate that when appropriate alternate prey are available, the juxtaposition of two juvenile year-classes can occur without cannibalism resulting. At station 95 in the eastern Bering Sea in August 1985, age-0 and age-1 pollock had a trophically neutral relationship: the food habits of each year-class did not impinge upon nor imperil the other.

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Diet Composition of Pilot Whales *Globicephala* sp. and Common Dolphins *Delphinus delphis* in the Mid-Atlantic Bight during Spring 1989

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Several species of marine mammals are found in large numbers along the eastern United States and are seasonally abundant in the Mid-Atlantic Bight (Kenny et al. 1983, Payne et al. 1984). Concentrations of pelagic fishes also occur in the Mid-Atlantic Bight area during winter and spring and are preyed upon by marine mammals, seabirds, and piscivorous fishes (Overholtz et al. 1991). Pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* are two of the more abundant marine mammals found in the area and potentially account for 30% of the total consumption of pelagic fishes by all cetaceans in the region (Overholtz et al. 1991). Detailed analyses of diet composition, specific rations, and size and age composition of prey consumed by marine mammals are sparse, since few healthy, recently dead animals are available for analysis. Most information on the diet composition of marine mammals found in the northwest Atlantic is from strandings, data from commercial whaling operations in Canada in the 1950s (Sergeant 1962), or incidental kills in commercial fishing operations.

Pilot whales were thought to feed extensively on short-finned squid *Illex illecebrosus* and secondarily on Atlantic cod *Gadus morhua* (Sergeant 1962, Mercer 1975), but more recently have been shown to feed on several other pelagic fishes and squids in the northwest Atlantic. In the area off New England and the Mid-Atlantic, pilot whales coincide with short and long-finned squid as well as Atlantic mackerel and butterfish *Peprilus triacanthus* (Smith et al. 1990). Pilot whales and common dolphins captured in foreign fishing operations during the 1980s were feeding on Atlantic mackerel and long-finned squid during winter and spring in the Mid-Atlantic region (Waring et al. 1990).

Studies quantifying fish consumption in the pelagic ecosystem off the eastern United States have suggested that marine mammals may be important predators (Kenny et al. 1983, Overholtz et al. 1991). Large numbers of marine mammals may reside in this region, but the impact of these predators on prey resources is difficult to assess since so few studies have documented the seasonal prey, ration size, and other dynamics of mammalian diets.

The objectives of this study were to describe prey types and quantities found in pilot whales and common dolphins, investigate the age distribution of their fish prey, and to assess the trophic role of these two mammals in the region. These data are necessary for understanding the sources and magnitudes of predation on fish resources at the age-specific level, a critical component of ecosystem modeling.

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Fishery Bulletin, U.S. 89:723–728 (1991).

Methods

Stomachs were collected from 5 pilot whales and 4 common dolphins that were taken incidental to fishing operations conducted in the Mid-Atlantic region of the eastern United States. Data were collected by U.S. observers on foreign vessels in the offshore Atlantic mackerel trawl fishery. Animals were obtained on five separate occasions from 19 March 1989 to 17 April 1989 in the Hudson Canyon area (Fig. 1). Sampling involved morphometric measurements of total length, girth, various fin and flipper measurements, determination of sex of the mammals, and excision of the stomach which was frozen for later analysis.

Contents of the thawed stomachs were sorted to the lowest taxonomic group possible and wet weights were obtained to the nearest gram. Individual fish were weighed separately, while squid were weighed as a group. Mantle length of squid was measured to the nearest mm (Lange and Johnson 1981). Fork length was recorded for mackerel to the nearest mm. Skull shape and otoliths were used to identify the Atlantic mackerel which were in various stages of digestion. Long-finned squid were identified by examining mantles, pens, and beaks. Mackerel were aged by mounting whole otoliths in resin and counting growth layers at 60× magnification (Dery 1988).

In some cases mackerel were fragmented usually at the caudal peduncle. Length of these specimens was estimated by realigning fragments or by visual reconstruction of the missing pieces through observations of fresher specimens along with a general knowledge of relative body proportions in the caudal region. Measurement error based on this method is unlikely to be greater than 10–20 mm (3–6% of total body length), and is accurate enough for estimating the relative

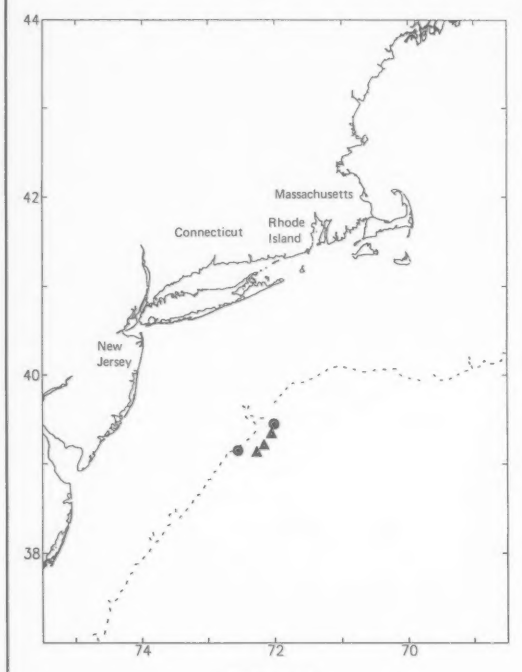

Figure 1

Mid-Atlantic region of the northeastern United States with locations in the Hudson Canyon area (north lat., west long.) of incidental captures of pilot whales (triangles) and common dolphins (circles) along the 100-m contour (dotted line) during March–April 1989.

size distribution of the prey. Partially digested mackerel were also weighed individually when possible, resulting in a minimum estimate of individual weight.

The food habits data were summarized to show diet characteristics of each animal. The age composition data for mackerel from stomach contents were summarized by percent number-at-age and compared with year-class size information from virtual population analysis (VPA) (unpubl. data) to discern if diet composition of the mammals was similar to age composition in the stock. To facilitate this comparison, a food selection index was calculated as

$$Li = ri - pi \quad (1)$$

where ri is the proportion of prey i in the stomach, and pi is the proportion of prey i in the environment (Strauss 1979). This index ranges from −1 to +1 with 0 indicating no predator preference (Strauss 1979).

In addition, the theoretical daily energy budget of each individual animal was compared with the estimated caloric value of the food in the stomach. Individual weights of pilot whales and common dolphins were obtained from length-weight equations (Lockyer 1991, J. Mead, Smithson. Inst., Wash. DC, pers. commun. 1989). Individual daily caloric requirements (Kcal/day) were estimated from a relationship between resting metabolism and body weight (Lockyer 1981), with a correction for assimilation and activity (Hinga 1979, Kenny et. al. 1983). The energy values of each animal's stomach contents were estimated by converting prey weight to caloric content (Kcal) by using conversion rates of 1.43 Kcal/g for Atlantic mackerel and 1.34 Kcal/g for long-finned squid (Steimle and Terranova 1985).

Results

Pilot whale and common dolphin fed on Atlantic mackerel and long-finned squid during March and April of 1989 (Table 1). A few otoliths of hake *Merluccius* sp. were found in two pilot whales and one common dolphin. The condition of prey items in both species ranged from slight to well digested, but could be identified to species. In contrast to previous years (Waring et al. 1990), none of the stomachs contained fresh material, although all the mackerel in pilot whale no. 1 were only slightly digested (Table 1). This suggests that all the animals had fed prior to being captured in the trawl.

The pilot whales that were examined were between 400 and 471 cm, both male and female (Table 1). Total weight of stomach contents in pilot whales were in the range 620–7200 g and averaged 2555 g (Table 1). Atlantic mackerel averaged 71% of the wet weight of stomach contents, and long-finned squid comprised the remaining (Table 1). Atlantic mackerel dominated the diets of individual pilot whales in terms of percent weight, except pilot whale no. 2 which fed exclusively on long-finned squid (Table 1). The estimated mean length of mackerel were in the range 355–460 mm, with mean weights of 332–426 g, and modal age of 7 years. (Table 1). Mean lengths of long-finned squid were 88–146 mm and weights 32–93 g, although both of these measurements are probably underestimates since all squid were at least partially digested.

The four common dolphins were also medium-sized individuals of 170–213 cm (Waring et al. 1990) of both sexes (Table 1). They fed primarily on mackerel, although the remains of long-finned squid were present in the stomachs of two individuals (Table 1). It was impossible to measure any mackerel found in the stomachs since they were well digested, and they were

Table 1

Summary of stomach contents of 5 pilot whales and 4 common dolphins collected in March–April 1989 off the northeastern United States. AM = Atlantic mackerel, LS = long-finned squid.

Predator				Prey									
				Species (*N*)		Modal age	Mean length (mm)[1]		Mean wet weight (g)		Total weight (g)[2]		% weight	
Species	Specimen no.	Length (cm)	Sex	AM	LS	AM	AM	LS	AM	LS	AM	LS	AM	LS
Pilot whales														
	1	401.0	M	16	4	7	354.8	88.3	426.8	93.3	6829.4	373.0	94.8	5.2
	2	400.0	F	—	43	—	—	145.8	—	52.8	—	2268.7	—	100.0
	3	463.0	F	1	8	—	460.0	102.0	359.4	32.8	359.4	262.6	57.8	42.2
	4	440.0	M	2	—	—	360.0	—	332.3	—	664.5	182.0	78.5	21.5
	5	471.0	F	3	13	7	378.3	128.8	424.6	43.3	1273.7	563.1	69.3	30.7
Total				22	68	7	363.2	134.0	414.9	51.0	9127.0	3649.4	71.4	28.6
Common dolphins[3]														
	1	170.0	M[4]	4	—	7	—	—	186.9	—	747.5	—	100.0	—
	2	207.0	F	6	—	7	—	—	403.3	—	2420.0	—	100.0	—
	3	200.0	M	4	—	5	—	—	294.3	—	1177.0	—	100.0	—
	4	213.0	M	3	—	7	—	—	113.0	—	339.0	—	100.0	—
Total				17	—	—	—	—	—	—	4683.5	—	100.0	—

[1] Only lengths of measurable prey are included here.
[2] Includes weight of all stomach contents for this species.
[3] Specimens 3 and 4 had long-finned squid pens in the stomach from a previous meal.
[4] Atlantic mackerel found in the stomachs could not be measured or weighed individually due to the state of digestion.

identified by otoliths. The estimated mean weight of mackerel was 113–403 g, and modal age was 7 years (Table 1).

The age distribution of mackerel was similar in pilot whales and common dolphins, with age groups 4–8 representing the bulk of the prey items. Age 7 was the dominant age group in the diet of both predators comprising 71% and 56% of the mackerel eaten by pilot whales and common dolphins, respectively (Table 2). This age group is from the very large 1982 year-class of mackerel (Table 2). Values from the food selection index comparing percent in stomachs with the stock, indicate that both predators may have concentrated on mackerel from age group 7. Positive index values were also obtained for ages 5–8 for common dolphins (Table 2).

A comparison of theoretical daily energy budgets of individual animals with the caloric content observed in stomach contents revealed that, in most cases, the diets represented only a small fraction of the daily requirement (Table 3). The amount of observed prey in pilot whale stomachs would supply 1.8–28% of the daily theoretical requirement, and 6–44% in common dolphins.

Discussion

Pilot whales and common dolphins captured during fishing operations for mackerel in 1989 appeared to feed primarily on mackerel and long-finned squid, although three specimens contained otoliths of hake *Merluccius* sp. Waring et al. (1990) reported on the diet of 33 common dolphins collected from 1986 to 1988 during the same time period and found similar prey items, including the presence of a few hake otoliths. Hake may either be consumed infrequently or the otoliths are entering the stomachs through other prey such as long-finned squid.

Capture location of the two mammal species was localized (Fig. 1), but captures extended over a 30-day period. The data may represent a normal pattern for winter-spring feeding or an attraction to fishing activity. This study suggests that the captured mammals were not entirely dependent on fishing operations for prey, since long-finned squid were present in stomachs but not in catches by commercial vessels.

Results from the food selection index analysis suggest a slight positive selection for ages 5,6, and 8 by common dolphins, and moderate selection for age 7 by both cetaceans (Table 2). Statistical tests are possible with this index (Ready et al. 1985); however, they

Table 2

Comparison of abundance of Atlantic mackerel in the sea with numbers in stomach samples from 5 pilot whales and 4 common dolphins taken incidentally during March–April 1989 off the northeastern United States.

	Mackerel			Pilot whales			Common dolphins		
Age	Year-class	Abundance[1]	% of population	*N*	% in stomachs	Li[2]	*N*	% in stomachs	Li[2]
2	87	584	14.4	0	0.0	−0.144	0	0.0	−0.144
3	86	471	11.6	1	4.8	−0.068	0	0.0	−0.116
4	85	823	20.3	2	9.5	−0.108	1	6.3	−0.140
5	84	199	4.9	0	0.0	−0.049	2	12.5	0.076
6	83	107	2.6	1	4.8	0.022	2	12.5	0.099
7	82	1538	38.0	15	71.4	0.334	9	56.3	0.183
8	81	245	6.1	1	4.8	−0.013	2	12.5	0.064
9	80	38	0.9	0	0.0	−0.009	0	0.0	−0.009
10	79	5	0.1	0	0.0	−0.001	0	0.0	−0.001
11	78	30	0.7	0	0.0	−0.007	0	0.0	−0.007
12	77	4	0.1	0	0.0	−0.001	0	0.0	−0.001
13	76	7	0.2	1	4.8	0.046	0	0.0	−0.002
Total		4051	100.0	21[3]	100.0		16[3]	100.0	

[1]Millions of fish (unpubl. data).
[2]Linear index of food selection (Strauss 1979).
[3]Numbers reported here are 1 less than in Table 1, because 1 fish from each cetacean could not be aged.

Table 3

Comparison of daily estimated ration with amount of food in stomachs for 5 pilot whales and 4 common dolphins taken incidentally during March–April 1989, off the northeastern United States. AM = Atlantic mackerel, LS = long-finned squid.

	Predator				Prey					
					Total weight (g)		Caloric content[3] (Kcal)			
Species	Specimen no.	Length (cm)	Weight[1] (kg)	Ration[2] (Kcal/day)	AM	LS	AM	LS	Total caloric content (Kcal)	% of ration
Pilot whale										
	1	401.0	760	37184	6829.4	373.0	9766	500	10266	27.6
	2	400.0	725	35844	—	2268.7	—	3040	3040	8.5
	3	463.0	1049	47841	359.4	262.6	514	352	866	1.8
	4	440.0	957	44541	664.5	182.0	950	244	1194	2.7
	5	471.0	1095	49487	1273.7	563.1	1821	755	2576	5.2
Common dolphin										
	1	170.0	62	5236	747.5	—	1069	—	1069	20.4
	2	207.0	104	7850	2420.0	—	3461	—	3461	44.1
	3	200.0	94	7253	1177.0	—	1683	—	1683	23.2
	4	213.0	110	8203	339.0	—	485	—	485	5.9

[1]Obtained from a length-weight relationship from Lockyer (1991) for pilot whales, and from J. Mead (Smithson. Inst., pers. commun. 1989) for common dolphins.
[2]From a relationship between resting metabolism and body weight (Lockyer 1981) and a correction for assimilation and activity (Kenny et al. 1983).
[3]Obtained by converting prey weight to Kcal by using 1.43 Kcal/g for Atlantic mackerel and 1.34 Kcal/g for long-finned squid (Steimle and Terranova 1985).

cannot be used on these data since current methodology is not available to calculate the variance of stock size estimates based on the VPA. Mackerel school by size-age groups, and the older fish tend to be distributed farther offshore than younger fish (Sette 1950). The observed feeding pattern may reflect the absence of smaller, younger fish offshore and low abundance of older, larger fish (Table 2).

The age distribution of mackerel in the diet indicates that these smaller odontocetes are probably feeding on the older age groups of mackerel during the winter–spring season (Table 2). This is in contrast to fish predators such as Atlantic cod and spiny dogfish *Squalus acanthias* that feed on younger age groups of mackerel (Overholtz et. al. 1991). Smaller mouth size of the predatory fish probably limits their prey size. Marine mammals can feed on larger prey and are in direct competition with fisheries targeting these older, larger fishes (Overholtz et. al. 1991).

Energy budget calculations, when compared with caloric values of stomach contents, indicate that both pilot whales and common dolphins may need to feed several times per day to obtain their needed ration (Table 3). Although the analysis may be biased low and therefore somewhat conservative, it does suggest that the observed stomach contents may represent only a percentage of estimated daily requirement (Table 3). Therefore, stomach data from these cetaceans may underestimate the actual impact on prey resources.

The role of marine mammals has not been adequately described in many ecosystems since many populations are remote and the autopsy of fresh animals is infrequent. In the northwest Atlantic, most information on the diet composition of cetaceans has come from stranded incidentally captured animals, and commercial harvests (Sergeant 1962, Mercer 1975, Sergeant et al. 1980) or observations of codistributed mammals and prey (Overholtz and Nicolas 1979, Payne et al. 1986, Mayo et al. 1988, Smith et al. 1990). In the future, collection of more data on feeding behavior, prey species consumed, and overlapping distributions of mammals and prey on a seasonal basis, as well as a thorough sampling of incidental captures, will be necessary if the trophic role of marine mammals is to be determined. An intensive survey of the entire mammal population during this winter-spring period and in other seasons, along with some observations of activity around fishing vessels, would help determine how important the mackerel fishery is in influencing the behavior of smaller cetaceans.

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Relation between Hook Depth and Fishing Efficiency in Surface Longline Gear

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Surface longline gear can operate at a range of depths, and hooks placed at different depths can have different fishing efficiencies, depending on the target species and its behavior. With better knowledge of the relationship between hook depth and hook catch rates, catch rates could be improved by placing the majority of hooks at the depth range preferred by the target species. However, little data exist on this subject in the literature, probably due to the difficulty of obtaining information about the differential catch rates of each hook and in estimating absolute depths. Yoshihara (1951) reports that the vertical distributions of *Thunnus orientalis* and *Germo germo* caught by longline are bell-shaped, suggesting different water temperature preferences by each species. Suzuki et al. (1977) state that the same fishing methods and longline gear are frequently used regardless of the areas and species. These authors also remark that there have been no systematic studies on the vertical distribution of tunas and billfishes. A well-known exception was in the 1970s when the Korean and Japanese commercial longliners changed from regularly using the gear near surface to fish for bigeye tuna to using it at greater depths to target yellowfin tuna *Thunnus albacares* (Saito 1975, Suzuki et al. 1977, Yang and Gong 1987). There is also some information about the behavior and depth range of swordfish *Xiphias gladius* (Carey and Robison 1981) and blue shark *Prionace glauca* (Sciarrota and Nelson 1977) in the literature.

Our aim was to obtain a simple, statistical relationship between the fishing efficiency of each hook in a basket (a stretch of longline between two floats) and its relative depth. We used data from a tropical eastern Atlantic Ocean fishing trip, where commercial longline gear was regularly used by southern Spanish fishermen to catch swordfish as a primary target species and mako shark *Isurus oxyrinchus* as the most valuable bycatch species. The study was carried out on the gross catch, in which the target species, swordfish and mako shark, comprised only 5–21% of the total catch.

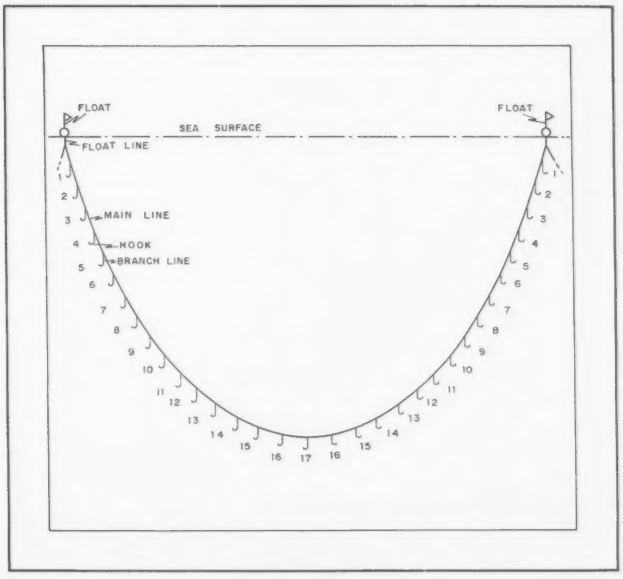

Figure 1
Scheme of the longline used in this study. Numbers show hook position.

Methods

The longline gear employed in this study consisted of "baskets" between floats (Fig. 1). Float lines measured about 7 m, while the main line within each basket measured about 1200 m. Branch lines (33 per basket) were 15 m long. This standard gear design is modified by

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Spanish fishermen operating in the Atlantic Ocean and Mediterranean Sea according to their experience and customs.

A total of 706 baskets were deployed during 16 nocturnal fishing operations in April 1985, located between 10°27′–11°42′N lat. and 17°17′–17°45′W long. Each fish was identified, sexed, and measured. The hook number within each basket was also recorded. A summary of the species caught and their abundances will be reported in a separate paper (Rey and Muñoz-Chápuli, in press).

Maximum depth reached by the deepest hook (position 17) was estimated to be between 370 and 460 m, using the theoretical procedure described by Yoshihara (1951, 1954).

Hook catch rates (HR) per 100 hooks were calculated using:

$$HR = (\text{number of fish caught/number of hooks set in the } j\text{th position}) \times 100.$$

A total of 1412 hooks were set in positions 1–16, while 706 hooks were set in position 17.

Results and discussion

Table 1 shows the hook catch rates (HR) obtained for total catch, swordfish, and mako shark which was the most valuable species in the bycatch. Composition of bycatch is also presented in this table. A maximum HR of more than 5 fish/100 hooks for the total catch was observed between hook positions 3 and 5 (Fig. 2A). Values were generally lower beyond position 10, where the HR values were 2.8–4.6 fish/100 hooks.

The highest HR for swordfish was recorded at hook positions 3–13 (Fig. 2B). Mako sharks were captured mainly between hook positions 5 and 8 (Fig. 2C). They were never captured at hook position 15 or 17.

Table 1 includes the proportion of bycatch (total catch less swordfish and mako shark). As can be observed in Figure 2D, hook positions 14–17 show the highest HRs for the bycatch proportion. This indicates that these lower hooks are less effective for catching both swordfish and mako shark, which are caught in higher numbers on hooks 3–13.

Few data exist in the literature to compare with our results. Suzuki et al. (1977) compared catches of regular (to 150 m depth) and deep (250–300 m depth) tuna longlines in the western and central equatorial Pacific Ocean. They recorded a higher HR for swordfish using shallower gear. Carey and Robison (1981) observed, through radio-tracking, that in the Atlantic Ocean swordfish follow isoluminic trajectories. They were located in depths of 400–600 m during the day and 0–170 m at night. However, in the Pacific Ocean the depth range recorded for swordfish was 50–100 m during the day and 0–70 m at night. This could explain the slightly deeper maximum depth of fishing efficiency we recorded in the tropical eastern Atlantic Ocean, compared with that of Suzuki et al. However, Yang and Gong (1987) found a higher swordfish catch per unit of effort around 150 m in the central Atlantic (0°–10°N).

Table 1

Hook catch rates of total fish, swordfish *Xiphias gladius*, and mako shark *Isurus oxyrinchus* during 16 nocturnal fishing operations in the tropical eastern Atlantic Ocean. Right column shows proportion of "other species" in the total catch. Correlation coefficients (r) from the linear relationship between hook position and HR/proportion other species are also shown. HR = no. hooks with catch/no. hooks set in jth position × 100 (see text).

Hook position	Hook catch rates (fish taken/100 hooks)				Proportion of other species (%)
	Total fish	Swordfish	Mako shark	Other species*	
1	4.46	0.35	0.28	3.83	86
2	4.18	0.35	0.21	3.62	87
3	5.67	0.92	0.21	4.54	80
4	5.10	0.57	0.21	4.32	85
5	5.24	0.64	0.35	4.25	81
6	4.39	0.42	0.07	3.90	89
7	4.96	0.71	0.28	3.97	80
8	3.68	0.42	0.35	2.91	79
9	4.81	0.57	0.14	4.10	85
10	4.81	0.57	0.21	4.03	84
11	3.47	0.50	0.21	2.76	80
12	4.53	0.64	0.21	3.68	81
13	4.18	0.64	0.07	3.47	83
14	3.68	0.07	0.21	3.40	92
15	4.60	0.50	0.00	4.10	89
16	3.89	0.42	0.07	3.40	87
17	2.83	0.14	0.00	2.69	95
r	−0.59**	−0.35	−0.63**		0.43

* 55.9% *Carcharhinus signatus*, 17.0% *C. falciformis*, 9.3% *Alopias superciliosus*, 7.8% *Prionace glauca*, 5.5% *Mobula* sp., 1% *Sphyrna lewini*. Less than 1%: *Sphyrna couardi, S. mokarran, S. zygaena, Centrophorus granulosus, Galeocerdo cuvieri, Isurus paucus, Carcharhinus plumbeus, Thunnus obesus, Lepidocybium solanderi, Alepisaurus ferox.*

** $P<0.01$.

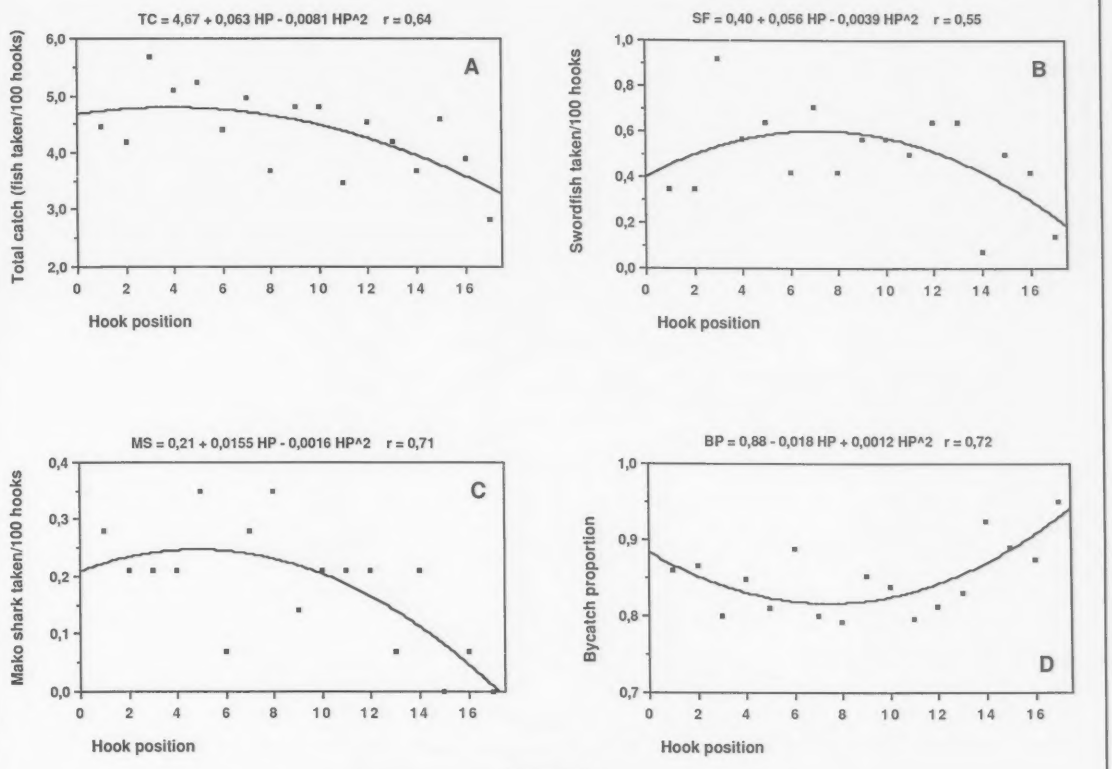
TC = 4,67 + 0,063 HP - 0,0081 HP^2 r = 0,64
Total catch (fish taken/100 hooks)
Hook position
A
SF = 0,40 + 0,056 HP - 0,0039 HP^2 r = 0,55
Swordfish taken/100 hooks
Hook position
B
MS = 0,21 + 0,0155 HP - 0,0016 HP^2 r = 0,71
Mako shark taken/100 hooks
Hook position
C
BP = 0,88 - 0,018 HP + 0,0012 HP^2 r = 0,72
Bycatch proportion
Hook position
D

Figure 2

Relationships of hook catch rates to hook position for the total catch (A), swordfish (B), and mako shark (C). (D) Relationship between bycatch proportion (total catch less swordfish and mako shark) and hook position.

The ratios described in the results suggest that a better catch could be obtained with a different basket shape. Thus, by eliminating the deepest hooks, a smaller basket would be produced with most of the hooks placed in the depth range that demonstrated better fishing efficiency.

It should be noted that these data are valid only for particular spatial-temporal conditions, and they depend on environmental and biological variables such as temperature, light level, current, behavior, and food availability. Notwithstanding, our results show that further comparative and experimental studies on longline gear design could significantly improve the yield of fishing operations.

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Growth and Mortality of King Mackerel *Scomberomorus cavalla* Tagged in the Southeastern United States

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King mackerel *Scomberomorus cavalla* is a heavily exploited coastal pelagic scombrid that has received considerable attention from research and management concerns throughout the southeastern United States (Gulf of Mexico and South Atl. Fish. Manage. Counc. 1985). Age-length data from analyses of otoliths have recently been used to estimate growth and mortality of the Gulf of Mexico migratory ("stock") group (Manooch et al. 1987) and growth of the Atlantic group (Collins et al. 1988). Previous studies did not differentiate between Gulf and Atlantic groups (Beaumariage 1973, Johnson et al. 1983). Length-increment (tag return) data can also be used to estimate growth and mortality; however, the growth parameter values generated from these data may not be directly comparable with those developed using age-length information (Francis 1988). In this report, we present estimates of growth and mortality based on mark-recapture data for both the Gulf and Atlantic king mackerel groups.

Table 1

Number of king mackerel *Scomberomorus cavalla* tag releases off southeastern United States by year, 1975–79, and migratory group.

	Location and month of release/Migratory group			
Year	Ft. Pierce, FL December–March/ Gulf of Mexico[1]	Florida Keys February, March/ Gulf of Mexico[2]	Jupiter, FL May, June/ Atlantic[3]	S. Carolina May, June/ Atlantic[4]
1975	880	–	372	–
1976	1904	974	1318	–
1977	1666	844	588	–
1978	1966	776	396	–
1979	–	–	–	809
Total	6416	2594	2674	809

[1] For all years except 1975, the annual totals for the Ft. Pierce area include December releases of the previous year. Northern boundary of the release area was defined by 28°45′N lat. and the southern boundary by 27°07′N lat.
[2] Eastern boundary of the release area was defined by 81°10′W long., southern boundary by 24°10′N lat., western boundary by 83°30′W long., and northern boundary (Gulf of Mexico only) by 27°00′N lat.
[3] Northern boundary of the release area was defined by 27°07′N lat. and southern boundary by 26°19′N lat.
[4] Northern boundary of the release area was defined by 33°50.0N lat. and southern boundary by 32°03.0′N lat.

Methods

King mackerel captured by hook-and-line were marked with internal anchor tags along the southeastern United States from South Carolina to the Florida Keys during 1975 to 1979 (Sutter et al. 1991). Tagged fish were assigned to the Gulf or Atlantic migratory groups (Table 1) based on location and date of release using current stock definitions (Powers and Eldridge 1983). King mackerel tag returns that did not show negative growth (based on reported length) were grouped into 30-day intervals based on time-at-large. The mean change in length between release and recapture and the mean time-at-large were determined for each 30-day period. Use of means within blocks eliminated the unequal weighting caused by the large number of fish returned less than one year after release, or by any periodicity in seasonal recaptures. These values were used to estimate the von Bertalanffy growth parameters L_∞ (asymptotic size) and K (growth rate constant) using a non-linear solution (SAS 1985) of Fabens (1965) method. We did not have enough fish to partition our data further to describe growth parameters for male and female king mackerel.

Mortality estimates were made separately for Gulf of Mexico and Atlantic king mackerel groups.

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Table 2

Tag-recapture matrix for Gulf of Mexico and Atlantic migratory groups of king mackerel *Scomberomorus cavalla*. Year reported represents a 12-month time interval from time of release.

Year released	No. released	Year reported 76/77	77/78	78/79	79/80	80/81	81/82	82/83	83/84
Gulf of Mexico group									
1976	2878	120	58	26	7	4	3	—	—
1977	2510		108	62	22	12	3	—	—
1978	2742			104	66	25	12	8	2
Atlantic group									
1976	1318	34	15	7	6	2	—	—	—
1977	588		25	16	12	8	3	—	1
1979	809				12	14	7	6	1

Regression analysis techniques (Gulland 1969) were used to estimate the average annual survival rate for each tagging year by grouping returns into 12-month intervals beginning with month of release (December–March for the Gulf of Mexico group, and May–June for the Atlantic group) (Table 2). Fish recaptured within 30 days of release were not included in our analysis, which allowed tagged fish to recover from tagging and reduced the effect of short-term tagging mortality on our estimates of survival rate. Only the Gulf stock had sufficient numbers of recaptured fish to use the method of Brownie et al. (1985) to estimate annual survival.

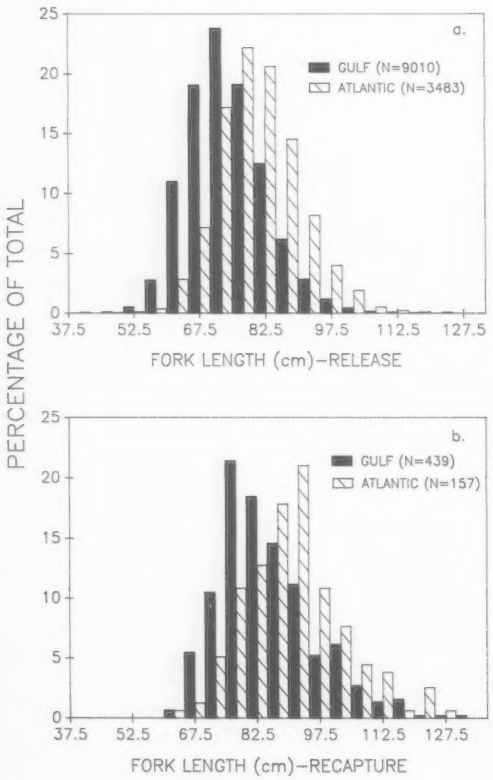

Figure 1

Length-frequencies of king mackerel *Scomberomorus cavalla* at release and recapture from Gulf of Mexico and Atlantic migratory groups. Fish were grouped by 50 mm FL intervals; mid-range values are used for each plot.

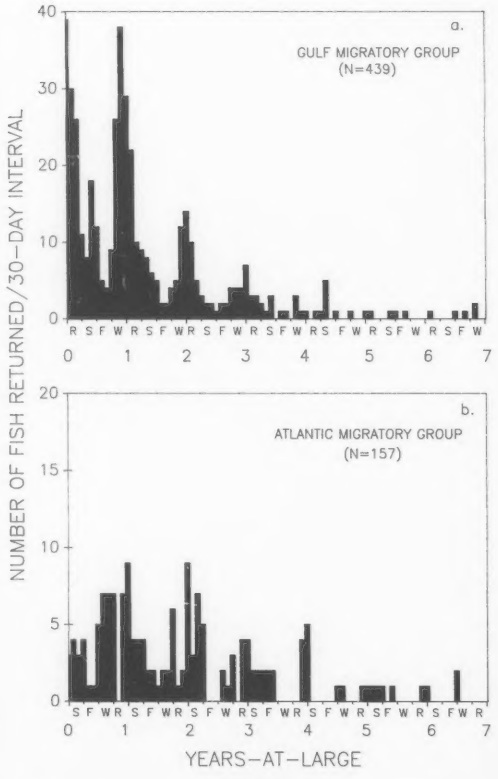

Figure 2

Recaptured king mackerel *Scomberomorus cavalla* utilized in the growth analysis, summarized by 30-day blocks from time of tagging, for the Gulf of Mexico (released during December–March) and Atlantic (released during May–June) migratory groups. Seasons for each year of recapture are: W = winter, R = spring, S = summer, and F = fall.

Table 3

Summary of theoretical growth parameters (L_∞, K) and mortality estimates (Z), sexes combined, for Gulf of Mexico and Atlantic migratory groups of king mackerel *Scomberomorus cavalla*.

Study	Migratory group	Interval	L_∞ (cm)	K	Z
Present study	Gulf of Mexico	1975–88[1]	132.6	0.127	0.794 (1976–82[2]) 0.877 (1977–82[2]) 0.766 (1978–84[2])
	Atlantic	1975–85[1]	152.0	0.070	0.658 (1976–82[2]) 0.493 (1977–82[2]) 0.582 (1979–84[2])
Manooch et al. (1984)	Gulf of Mexico	1980–85	147.8	0.115	0.54 (1980[3]) 0.72 (1981[4]) 0.50 (1984[5])
Collins et al. (1988)	Atlantic	1983–87	112.7[6] 127.7[7]	0.213[6] 0.087[7]	Not available

[1]Time from release to recapture used in calculating growth parameters.
[2]Years used in regression analysis of recaptured king mackerel.
[3]Year fish collected from recreational hook-and-line catches in northwest Florida.
[4]Year fish collected from gillnet catches in south Florida.
[5]Year fish collected from south Florida purse-seine catches.
[6]Whole otoliths.
[7]Sectioned otoliths.

Results and discussion

Growth analysis

A total of 9010 king mackerel from the Gulf of Mexico king mackerel migratory group were tagged; 794 were reported recaptured, and 439 fulfilled our criteria for inclusion in the growth analysis. The mean length-at-tagging was 74.5 cm FL (SD 8.92 cm, range 42.5–120.0 cm) (Fig. 1a), while the mean length-at-return was 85.2 cm FL (SD 11.61 cm, range 62.5–133.0 cm) (Fig. 1b). Maximum time-at-large was 10.48 years (3829 days), with a mean of 1.06 years (SD 1.24 yr). Fish were recaptured most frequently during the first year of freedom (51.5%), with seasonal increases in returns noted during winter and spring months (Fig. 2a). We recaptured Gulf of Mexico migratory group fish from Texas to southeast Florida through 1988, although 95.5% were taken before 1981.

The relationship between length-at-return minus length-at-tagging ($\Delta\ell$) vs. number of days-at-large (Δt) for Gulf of Mexico king mackerel was described by: $\Delta\ell = 3.722 + 0.012\ (\Delta t)$ (r^2 0.503; df 1, 438; $P<0.01$). Mean values from a total of 63 30-day blocks were used to generate an estimate of $L_\infty = 132.6$ cm FL (95% CI 114.3–150.8 cm), and K = 0.127 (95% CI 0.068–0.186). Manooch et al. (1987) used whole otoliths to calculate an L_∞ value of 147.8 cm (95% CI 131.6–164.0 cm) and K = 0.115 (95% CI 0.079–0.152) for Gulf of Mexico king mackerel captured during 1980–85 (the majority taken from Key West, northwest Florida, and Texas), combining both sexes (Table 3). Growth parameters determined from our tagging study overlap the spatial and temporal constraints of their age-length data.

A total of 3483 king mackerel were tagged from the Atlantic king mackerel migratory group. Recaptures were reported for 253 fish, of which 157 provided sufficient data for our growth analysis (Fig. 1b). Mean length-at-tagging was 81.0 cm FL (SD 9.17, range 50.0–122.5 cm), while the mean length-at-return was 91.0 cm FL (SD 11.65, range 64.8–127.0). The maximum time-at-large was 6.47 years (2361 days), with a mean of 1.56 years (SD 1.41 yr). Fewer returns were reported during the first year of freedom (31.2%) than were noted for the Gulf migratory group (Fig. 2b), and most returns occurred during the summer and fall. We recaptured Atlantic migratory-group king mackerel through 1985; however, 92.1% were taken before 1982, prior to commercial and recreational quota restrictions.

The relationship between growth ($\Delta\ell$) and time-at-large (Δt) for the Atlantic fish is: $\Delta\ell = 4.057 + 0.008\ (\Delta t)$ (r^2 0.323; df 1, 156; $P<0.01$). The estimated asymptotic length for Atlantic king mackerel calculated from 52 30-day blocks was 152.0 cm FL (95% CI 87.3–216.8 cm), with an associated K = 0.070 (95% CI 0.005–0.146). Collins et al. (1988) used whole and sectioned otoliths from king mackerel in the Atlantic group to calculate estimates of $L_\infty = 112.7$ and 127.7 cm FL, and K = 0.213

and 0.087 (whole vs. sectioned, respectively) for fish collected from Cape Canaveral, Florida, to Cape Fear, North Carolina, during 1983–87 (Table 2). They concluded, however, that whole otoliths may have provided biased estimates, at least for Atlantic king mackerel. Although the spatial distribution of our tagging effort was similar to the geographical study area of Collins et al. (1988), their collections occurred during regulation of the king mackerel fishery.

Comparison of our growth estimates for Gulf and Atlantic king mackerel should be made with caution due to our limited sample size and our reliance on reported fish lengths. The Atlantic group appears to exhibit a larger maximum size (L_∞) and a slower relative growth rate (K) than its Gulf of Mexico group counterparts (Table 2). This is supported by comparing the two regression equations of growth ($\Delta\ell$) vs. time-at-large (Δt). We found that the slope for the Gulf of Mexico group was significantly different (ANCOVA; F 7.344, df 1, 592; $P<0.01$) than that observed for the Atlantic king mackerel, indicating a faster growth rate over the size range that were tagged and recaptured.

Growth analyses using age-length data provide an estimate of asymptotic mean length-at-age, while mark-recapture data provide estimates of the maximum length achieved in the population (Francis 1988). Our L_∞ estimate for the Gulf of Mexico migratory group (132.6 cm) was larger than that for any individual fish tagged or returned, except for one fish which was 133.0 cm FL; however, Trent et al. (1987) found fish as large as 158.0 cm FL in their work off Louisiana. These large fish were females taken from what may be a year-round resident population (Fable et al. 1987) which was not included in our tagging efforts. Fish from the Gulf of Mexico migratory group that were tagged in our study would therefore be considered part of the 'small' migratory fish described by Fable et al. (1987). Manooch et al. (1987) reported sampling fish up to 180.2 cm FL from the Gulf of Mexico; however, because they did not provide a length distribution, the frequency of fish larger than 132.6 cm FL in their samples could not be determined. All fish collected from both the Collins et al. (1988) and our study were smaller than the calculated L_∞ values for the Atlantic migratory group.

Annual survival rates

Between 1976 and 1984, estimates of survival rates were lower for the Gulf migratory group than those observed for the Atlantic migratory group of king mackerel (Table 3). Regression and maximum-likelihood techniques yielded similar estimates of survival rates for the Gulf group. Annual pooled estimates of survival rates of these fish were in the range 41.6–46.5% (Z 0.877–0.766/yr; Table 3). The simplest model of Brownie et al. (1985; Model 3, constant survival and recovery rates, independent of age) was the most applicable to our database for the Gulf group of king mackerel, yielding a pooled estimate of 42.290 (SE 1.60; Z 0.794/yr). Estimates of annual survival rates for the Atlantic migratory group were in the range 51.8–61.1% (Z 0.658–0.493/yr).

Previous estimates of annual survival rates generated from age-length data compare favorably with those calculated from our mark-recapture data. Manooch et al. (1987) calculated instantaneous total mortality estimates from age-length data for king mackerel from two locations in the Gulf of Mexico that overlapped with our study area (Table 3). Their estimates of annual survival rates were in the range 48.7–60.7% (Z 0.719–0.499/yr) for king mackerel (both sexes combined) in south Florida collected during 1981 (gillnet) and 1984 (purse seine). King mackerel collected from recreational hook-and-line catches in northwest Florida during 1980 yielded an annual survival rate estimate of 58.3% (combining sexes; Z 0.540/yr). A pooled estimate of annual survival rate for king mackerel collected during 1977–79 along both the Gulf and Atlantic coasts was 63.0% (Z 0.462/yr; Johnson et al. 1983).

Growth and mortality estimates generated from age-length and length-increment studies must account for behavioral characteristics germane to a migratory species. King mackerel have been shown to have at least two migratory patterns along the southeastern United States; however, there is a seasonal overlap of the two groups along southeast Florida that may be as high as 29.4–41.8% (Sutter et al. 1991). Resident populations of king mackerel may also exist in the northcentral Gulf of Mexico (Fable et al. 1987) and in southeast Florida waters (Sutter et al. 1991). These factors should be considered when designing future survey strategies to describe growth and mortality rates.

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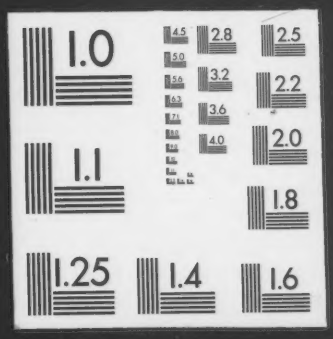
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